BIOLOGICAL REVIEWS

Cambridge Philosophical Society

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Biol. Rev. (2025), **100**, pp. 1635–1659.
doi: 10.1111/brv.70017

Lords of the flies: dipteran migrants are diverse, abundant and ecologically important

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ABSTRACT

Insect migrants are hugely abundant, with recent studies identifying the megadiverse order Diptera as the major component of many migratory assemblages. Despite this, their migratory behaviour has been widely overlooked in favour of more 'charismatic' migrant insects such as butterflies, dragonflies, and moths. Herein we review the available literature on dipteran migration to determine its prevalence, identify key migratory routes and elucidate areas that may prove fruitful for future research. Using 13 lines of evidence to determine migratory behaviour, we determined that species from 60 out of 130 dipteran families show evidence of migration, with Syrphidae fulfilling 12 of these criteria, followed by the Tephritidae with 10. By contrast, 22 families met just two criteria or fewer, underlining the need for more research into the migratory characteristics of these groups. In total, 592 species of Diptera were identified as potentially migratory, making them the most speciose group of insect migrants yet described. Despite this, only 0.5% of dipteran species were found to be migrants, a figure rising to 3% for the Syrphidae, a percentage mirrored by other migratory taxa such as butterflies, noctuid moths, and bats. Research was biased to locations in Europe (49% of publications) and while vast regions remain understudied, our review identified major flyways used by dipteran migrants across all biogeographic realms. Finally, we highlight an unsurpassed level of ecological diversity within dipteran migrants, including ecological roles of huge economic value. Overall, this review highlights how little is known about dipteran migration and how vital their migratory behaviour may be to the health of global ecosystems.

Key words: Diptera, migration, Syrphidae, ecological roles, global flyways, seasonal movement, conservation, insect movement, climate change, insect declines.

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I. INTRODUCTION

Each year, huge numbers of insects migrate globally to exploit seasonally available resources to increase their reproductive output, and/or escape habitat deterioration, e.g. due to temperature change, disease risk, food quality, or to seek overwintering sites (Chapman, Reynolds & Wilson, 2015; Dingle, 2014; Satterfield *et al.*, 2020). Some insects are known to migrate hundreds or even thousands of kilometres in a single journey (Hobson *et al.*, 2012), utilising the sun as a compass and favourable winds to facilitate their journeys (Gao *et al.*, 2020a; Knoblauch, Thoma & Menz, 2021; Massy *et al.*, 2021; Stefanescu *et al.*, 2013). Studies of insect migration have focussed mainly on the larger, more 'charismatic' insects such as moths, butterflies, and dragonflies (Chapman *et al.*, 2015; Menz *et al.*, 2022; Stefanescu *et al.*, 2013; Wikelski *et al.*, 2006; Guerra, Gegear & Reppert, 2014) or agriculturally/economically important species (Jia *et al.*, 2022; Jones *et al.*, 2019; Li *et al.*, 2020). Few have systematically analysed whole migratory assemblages. However, the studies that do exist have revealed a major group of migrants that remain hugely understudied and that are of great ecological importance: the Diptera (Hawkes *et al.*, 2022a, 2024).

The Diptera are a massive and megadiverse order of insects, consisting of over 125,000 described species, with some estimates suggesting numbers may easily surpass one million (Wiegmann *et al.*, 2011), indicating that a large percentage of all animal species are flies (Marshall, 2012). Dipteran migratory behaviour is poorly known and little studied, despite mass occurrences frequently being observed, including potentially two of the ten Plagues of Egypt described in the book of Exodus: gnats and dog-flies (Brenton, 1844). Likewise, in Serbian mythology, a legend concerning the death of a she-demon called a Hala that notes the spring arrival of a plague of Golubatz (*Simulum colombaschense*) flies from the rotting corpse (Карацић, 2005) suggests a basis for this legend within insect migration (Babic, Baranov & Ganslmayer, 1935). Recent systematic studies of insects passing through migratory bottlenecks have shown that Diptera can comprise nearly 90% of the individuals found in migratory assemblages in certain locations (Hawkes *et al.*, 2022a, 2024). Ecological assessments of these species suggest that they play a surprisingly large range of ecological roles compared to other migratory insect orders and are of major importance to economies and the natural world (Doyle *et al.*, 2020; Hawkes *et al.*, 2022a; Wiegmann *et al.*, 2011). However, when compared to other insect orders (e.g. Lepidoptera and Odonata), and particularly to vertebrates, very little is known and what information there is, is highly dispersed (Chowdhury *et al.*, 2021; Dingle, 2014).

In this review we synthesise knowledge on dipteran migration within the context of the wider migratory assemblage, to understand better the impact of this diverse group on global ecosystems. We collate all known information about dipteran migration globally including which families and species display migratory behaviour. We use this information to identify potential flyways, describe the ecological roles of these migrants, and explore the impacts that anthropogenically induced climate change may have on their migration.

II. DEFINING MIGRATION

A widely used definition of migration is one based on behavioural characteristics: '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' (Kennedy, 1985, p. 2). For dipteran migrants, and migratory insects in general, there are various viewpoints as to what constitutes migration (e.g. butterfly migration; Chowdhury *et al.*, 2021). Herein, we use the broad behavioural definition of migration quoted above, while recognising that currently we can only be certain of migratory behaviour in a few species. Instead of this representing a failure of the definition, this likely reflects a a lack of research into the migratory behaviour of Diptera and other insect taxa (Chowdhury *et al.*, 2021).

III. LITERATURE SEARCH

We searched *Google Scholar*, *Web of Science* and *PubMed* were searched to identify dipteran families with migratory behaviour based on at least one of the following 13 types of evidence [adapted from Chowdhury *et al.* (2021), to fit dipteran migrants better; see online Supporting Information Table S1 for details]: (*i*) seasonal back and forth movement; (*ii*) long-distance flight; (*iii*) seasonally appropriate directed movement; (*iv*) inability to develop in trapped habitat; (*v*) ability to choose favourable winds; (*vi*) mass arrival; (*vii*) capable of high-altitude flight; (*viii*) populations with a high rate of gene flow; (*ix*) strong flight capabilities (tethered flight mill); (*x*) orientation within a flight simulator; (*xi*) physiological/morphological changes in the migratory phenotype; (*xii*) seasonal appearance of a disease; and (*xiii*) unable to overwinter (in any state) in trapped location (Table 1).

To obtain an initial overview, we searched *Google Scholar* for articles published up to February 2023 using the search terms 'Diptera' and 'Migration' anywhere in an article, and excluded articles with the terms 'larvae' and 'cell' and 'development' to exclude evolutionary development studies. 'Dispersal' was also excluded as there are a large number of articles using this term that document small-scale (≤300 m) movements of Diptera. This methodology yielded 6200 results, of which a minimum of the abstract and results of the first 1000 papers were read carefully for relevance.

Table 1. Criteria used to establish presence of migratory behaviour in dipteran taxa. Criteria 1–4 form the 'core four' most often reported migratory characteristics. These migratory criteria are adapted from those used in Chowdhury *et al.* (2021) and are displayed as a heatmap against their occurrence in different dipteran families in Fig. 1.

Migratory criteria	Description	Example references
(1) Seasonal back and forth movement	Perhaps the strongest indicator of migration, the insects are observed during the springtime and then again in the autumn season. This can be evidenced by peaks in numbers in different migratory seasons (through radar data/citizen science recording, etc.) or by actively seeing the insects moving in one direction during one season, and then back in the opposite direction later in the year.	Florio *et al.* (2020)
(2) Long-distance flight	Long-distance flight is important for migratory insects to escape unfavourable habitats.	Hawkes *et al.* (2022a)
(3) Seasonally appropriate directed movement	Directed movement of an insect in a seasonally appropriate direction (e.g. towards higher latitudes in spring, towards lower latitudes in autumn) suggests a preferred flight detection.	Lack & Lack (1951)
(4) Inability to develop in trapped habitat	Larvae are incapable of developing due to unfavourable seasonal climate. This suggests that the adult insects must move away from their current location to lay their eggs in order for their young to survive.	Ashmole *et al.* (1983)
(5) Ability to choose favourable winds	An important factor in insect migration as the winds are used to assist their migrations.	Gao *et al.* (2020a)
(6) Mass arrival	Migratory flies often arrive in large numbers at the same time.	Hawkes *et al.* (2024)
(7) Capable of high-altitude flight	To migrate, flies often take advantage of higher altitude wind currents. There is little obvious reason for insects to be found consistently at higher altitudes if they are not attempting to move long distances.	Chapman *et al.* (2004)
(8) Populations with a high rate of gene flow	This suggests a high level of movement between populations by individuals.	Mignotte *et al.* (2021)
(9) Strong flight capabilities (tethered flight mill)	To migrate long distances, insects must have strong flight capabilities. This can be evidenced by their performance in a flight mill.	Nilssen & Anderson (1995)
(10) Orientation within a flight simulator	A preferred, seasonally advantageous flight direction in a flight simulator is indicative of migratory behaviour.	Massy *et al.* (2021)
(11) Physiological/morphological changes in the migratory phenotype	This includes any physiological or morphological changes associated with a migratory phenotype. This could include delaying the development of reproductive organs, or changes in morphology between resident and migratory generations.	Doyle *et al.* (2025)
(12) Seasonal appearance of a disease	If the insects are associated with seasonality of a disease, then it is likely that they are acting as vectors – bringing the disease from distant locations.	Nabeshima *et al.* (2009)
(13) Unable to overwinter (in any state) in trapped location	Adult insects are trapped in a region in which they are not capable of surviving the winter (e.g. at high latitudes, above oceans, in high mountain passes, etc.).	Ashmole *et al.* (1983)

A provisional list of migratory dipteran families ('X') was obtained from these papers, and *Google Scholar* was then searched for specific information on each of these families using the term 'X migration'. A specific search of dipteran families using 'X migration' was also carried out in both *Web of Science* and *PubMed* databases. In *Web of Science*, the search string 'Diptera migration NOT cell' yielded 700 results. In *PubMed* the same search string returned 993 results. To identify relevant studies that may not be included in online search databases due to age, manual searches were performed of the reference lists of books on insect migration such as Johnson (1969) and Williams (1958) and of the reference lists of relevant articles. We decided that saturation of the available literature was close to being reached when further searches of *Google Scholar*, *Web of Science*, and *PubMed* using the same search terms repeatedly returned irrelevant articles. In total 344 relevant articles were identified. Most were written in English, but when relevant articles in other languages were found (titles/abstracts automatically translated by the search engines), these were translated and included: French (seven articles), German (six), Japanese (three), and Portuguese, Danish, Chinese and Dutch (one article each).

IV. PREVALENCE OF MIGRATION

We found evidence for migration behaviour in approximately 47% of all dipteran families (60 out of 130) with data sourced from 344 papers (Fig. 1). Details of the articles and the migration categories for which they provide evidence can be found in Table S2. Syrphidae (hoverflies) were the most studied migratory dipteran family featuring in 48% of articles (recently reviewed by Reynolds *et al.*, 2024) and meeting the most migratory criteria: 12/13 (Fig. 1, and Table S2). The Tephritidae (fruit flies) met the second highest number of migratory criteria. Culicidae (mosquitoes) were the second best studied with 17% of the articles and, together with Muscidae (house flies), and Calliphoridae (blow flies and screw worms) and Chloropidae (grass flies), were one of four groups that met nine migratory criteria. All these families, even the minuscule Chloropidae (~2 mm in length), have been recorded as showing the 'core four' criteria (Table 1). Studies on Chloropidae have also shown they can choose favourable winds and fly at over 1500 m elevation (Hawkes *et al.*, 2024; Glick, 1939).

Drosophilidae (fruit flies), Mycetophilidae (fungus gnats), Anthomyiidae (root maggots) and Phoriidae (scuttle flies) fulfilled eight migratory criteria, including the core four. *Delia platura* (Anthomyiidae) have been recorded migrating in their millions from the Middle East to Cyprus along a northeast trajectory during the springtime, a journey involving an ocean crossing of at least 105 km (Hawkes *et al.*, 2022a). Simuliidae (black flies), Chironomidae (non-biting midges), Sphaeroceridae (small dung flies), Sciaridae (black fungus gnats) and Tipulidae (crane flies) all met seven migratory criteria with Simuliidae, Chironomidae, and Tipulidae meeting the core four criteria. For Tipulidae, there is evidence for seasonal back and forth movement at high altitude above Mali, and records from oil rigs in the North Sea (Hardy & Cheng, 1986; Keaster *et al.*, 1996) or in nets on ships in the Gulf of Mexico (Keaster *et al.*, 1996) that indicate long-distance flight across large expanses of ocean. Additionally, Gatter (1977) recorded Tipulidae utilising favourable winds in large numbers to migrate through the mountains of south-west Germany.

Five families fulfilled six migratory criteria with Sepsidae (ant-like scavenger flies), Dolichopodidae (long-legged flies) and Tachinidae (tachinid flies), meeting the 'core four' criteria. In this group the Ceratopogonidae (biting midges), were recorded undertaking seasonal back and forth movement at high altitude (Florio *et al.*, 2020) and long-distance flight above oceans (Keaster *et al.*, 1996).

Six families met five migratory criteria, with only Ulidiidae (picture-winged flies), fulfilling the core four criteria (Florio *et al.*, 2020; Keaster *et al.*, 1996; Beebe, 1951).

Four families met four migratory criteria: but none recorded the core four criteria. Despite this, all were recorded in areas unsuitable for larval development. For example, Bibionidae (march flies), were recorded after a migration fallout in snowfields (Ashmole *et al.*, 1983). Additionally, Bibionidae have been recorded displaying seasonally adaptive directed movement in large numbers (Beebe, 1951). On May 29th, 1948, Beebe (1951, p. 251) noted a *Bibio* sp. moving through a mountain pass accompanied by a 'veritable mist of others'. Eight families met three migratory criteria with 'long-distance flight', 'inability to develop in trapped habitat', and 'capable of high-altitude flight' the most common criteria met (Sparks *et al.*, 1986; Wolf *et al.*, 1986; Glick, 1939).

The largest group (12 families) met two migratory criteria, typically 'high-altitude flight'. For example, Asilidae (robber flies) have been recorded at medium–high altitude and showed seasonally appropriate directed movement (Glick, 1939; Beebe, 1951). Finally, 10 families met just one migratory criterion, again with 'high-altitude flight' the most common criterion met. Within this group Oestridae (bot and warble flies), met the 'strong flight capabilities on a tethered flight mill' criterion with the reindeer warble fly *Hypoderma tarandi* flying for 31.5 h, with a longest continuous flight of 12 h (Nilssen & Anderson, 1995). This capacity must play a role in the insect's life history, likely for following their reindeer hosts on their own extensive migrations.

Evidence for potential migratory behaviour was found for 592 species (see Table S3 for a full species list), representing around 0.5% of identified dipteran species. In the family with the most evidence for migration, the Syrphidae, 205 (3.41%) of the known 6000 species migrate (Fig. 2). Other dipteran families (Glossonidae, Dryomyzidae, and Lonchopteridae) had a higher percentage of migrants, but low species numbers (<150 species) and meet three or less migratory criteria. Interestingly, among butterflies, a well-studied group of migratory insects, 3% of all species have been diagnosed as migratory (Chowdhury *et al.*, 2021) as have 3% of noctuid

Family	#	1	2	3	4	5	6	7	8	9	10	11	12	13
Syrphidae*: hoverflies	12	■	■	■	■	■	■	■	■	■	■	■		■
Tephritidae*: fruit flies	10	■	■	■	■		■	■	■	■	■	■		
Culicidae*: mosquitoes	9	■	■	■	■		■	■	■	■			■	
Muscidae*: house flies	9	■	■	■	■	■	■	■	■					■
Calliphoridae*: blow flies	9	■	■	■	■	■	■	■	■					■
Chloropidae*: grass flies	9	■	■	■	■	■	■	■				■		■
Drosophilidae*: fruit flies	8	■	■	■	■			■	■		■	■		
Mycetophilidae*: fungus gnats	8	■	■	■	■	■	■	■						■
Anthomyiidae*: root maggots	8	■	■	■	■	■	■	■						■
Phoriidae*: scuttle flies	8	■	■	■	■	■	■	■						■
Simuliidae*: black flies	7	■	■	■	■		■	■	■					
Chironomidae*: non-biting midges	7	■	■	■	■		■	■						■
Sphaeroceridae: small dung flies	7		■	■	■	■	■	■						■
Sciaridae: black fungus gnats	7	■		■	■	■	■	■						■
Tipulidae*: crane flies	7	■	■	■	■	■	■	■						
Sepsidae*: ensign flies	6	■	■	■	■		■	■						
Ceratopogonidae: biting midges	6	■	■		■		■	■					■	
Dolichopodidae*: long-legged flies	6	■	■	■	■		■	■						
Tachinidae*: tachinid flies	6	■	■	■	■		■	■						
Tabanidae: horseflies	6		■	■	■		■	■		■				
Lauxaniidae: lauxanid flies	5	■		■	■		■	■						
Cecidomyidae, ephydridae	5	■	■		■		■	■						
Stratiomyidae: soldierflies	5		■	■	■			■		■				
Scathophagidae: dung flies	5		■	■	■		■	■						
Ulidiidae*: picture-winged flies	5	■	■	■	■			■						
Milichiidae: freeloader flies	4	■	■		■			■						
Agromyzidae: leaf-miner flies	4				■		■	■						■
Bibionidae: march flies	4			■	■		■	■						
Empidae: dagger flies	4		■		■		■	■						
Pallopteridae: flutter flies	3		■	■			■							
Lonchopteridae: spear-winged flies	3			■		■	■							
Micropezidae: stilt-legged flies	3		■	■	■									
Psychodidae, Sarcophagidae, Sciomyzidae, Platypezidae, Asteiidae	3		■		■			■						
Piophilidae: cheese flies	2				■		■							
Glossinidae: tsetse flies	2						■		■					
Curtonotidae, Diopsidae, Limoniidae, Lonchaeidae, Pipinculidae, Platystomatidae, Rhiniidae	2	■						■						
Asilidae, Therevidae	2			■				■						
Dryomyzidae: dryomyzid flies	2	■			■									
Pyrgotidae, Rhagionidae, Polleniidae	1			■										
Oestridae: bot and warble flies	1									■				
Scatopsidae, Bombyliidae, Scenopenidae, Heleomyzidae, Chamaemyiidae, Anisopodidae	1							■						

Fig. 1. Migratory criteria (see Table 1) fulfilled by the 60 identified migratory families of Diptera. Heat map colours indicate the number of migratory criteria confirmed for each family, with orange being the most (12 criteria fulfilled) and dark blue the least (one criterion fulfilled). # indicates the total number of migratory criteria met. The 'core-four' criteria are: (1) Seasonal back and forth movement; (2) long-distance flight; (3) seasonally appropriate directed movement; and (4) inability to develop in trapped habitat. Families meeting the core-four are indicated by an asterisk (*). Other criteria are: (5) ability to choose favourable winds; (6) mass arrival; (7) capable of high-altitude flight; (8) populations with a high rate of gene flow; (9) strong flight capabilities (tethered flight mill); (10) orientation within a flight simulator; (11) physiological/morphological changes in the migratory phenotype; (12) seasonal appearance of a disease; and (13) unable to overwinter (in any state) in trapped location.

moths (Alerstam *et al.*, 2011) and bats (Fleming *et al.*, 2003). While this may imply a consistent pattern across taxa, more research is needed.

V. MECHANISMS OF FLY MIGRATION

To migrate long distances, flies, like other migrants, rely on a variety of mechanisms to propel and orient themselves on their journeys. Studies performed at migratory bottlenecks suggest that warmer temperatures, dry conditions, and the presence of favourable winds are important factors influencing migration intensity in Diptera (Hawkes *et al.*, 2022a, 2024). A radar study across southern Britain showed that in the autumn, Syrphidae actively select winds that aid southward migration (Gao *et al.*, 2020a). During the springtime, Syrphidae and other Diptera have been recorded arriving at locations in Europe on winds from the south (Gao *et al.*, 2020a; Hawkes *et al.*, 2022a,b). Flying higher in favourable tailwinds allows

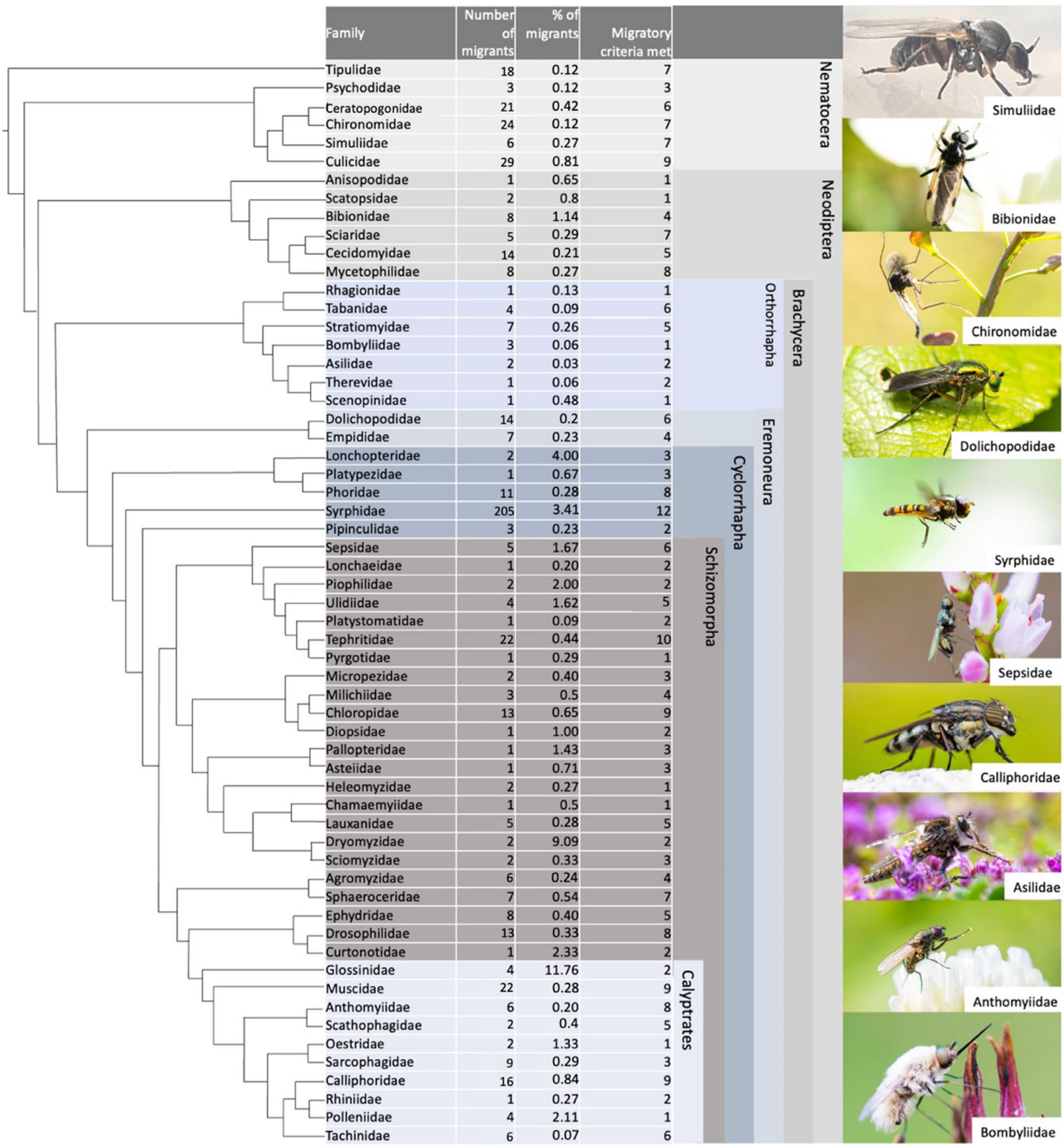

Fig. 2. Dipteran phylogeny showing the number of migrant species, the percentage of migratory species in each family, and the number of migratory criteria met. Phylogeny based on Wiegmann *et al.* (2011). All photographs ©Will Hawkes, apart from Simuliidae (©Mehmet Akif Suna).

migratory insects to fly faster than their self-powered airspeed (Chapman *et al.*, 2016; Gao *et al.*, 2020a). The speed of migratory Syrphidae above southern Britain has been recorded in the springtime at 40.3 km/h, and 35.3 km/h in the autumn (Gao *et al.*, 2020a), only a little slower than the speeds of nocturnal migrating moths (spring: 59.7 km/h, autumn: 49.5 km/h) and songbirds (spring: 48.5 km/h, autumn: 43.7 km/h) all speeds faster than their self-powered flight capability (Chapman *et al.*, 2016).

The selection of favourable winds and observations of directed movement points to the presence of a compass system within migratory Diptera. In tethered flight experiments, *Drosophila melanogaster* have been shown to maintain a constant flight heading utilising the sun and polarised light patterns (Warren, Giraldo & Dickinson, 2019; Weir & Dickinson, 2012). However, these headings are arbitrary with respect to a simulated sun and there is no evidence of time compensation as the sun moves across the sky (Warren *et al.*, 2019; Weir & Dickinson, 2012). A flight simulator experiment performed on two species of Syrphidae (*Scaeva pyrastri* and *Scaeva selenitica*) caught while migrating through the Pyrenees during the autumn, showed that these species utilise a time-compensated sun compass as seen in some Lepidoptera and birds, enabling them to maintain their preferred migratory heading even as the sun moves throughout the day (Massy *et al.*, 2021; Reppert, 2007; Åkesson & Bianco, 2017). The status of such a compass in other migratory Diptera remains to be investigated.

In addition to using environmental cues, Diptera, like other migrants, undergo changes to their physiology during migration (Chapman *et al.*, 2015; Bailleul *et al.*, 2012 Jenni & Schaub, 2003; Høgåsen, 1988; Southwood & Avens, 2010; Luschi *et al.*, 2007). These changes allow them to store energy and prepare for the long journey ahead. For example, flies will increase their fat stores before migrating, which provides them with the energy they need to fly long distances (Hondelmann & Poehling, 2007). The importance of this has been highlighted in flight mill studies in *Episyrphus balteatus* which demonstrate fuel reserves are a key determinant of distance flown and indicate that resource availability may play a major role in the success of migratory movements (Massy *et al.*, 2024). Changes in morphology and size are also common in insect migrants. While little evidence currently exists for dipteran migrants, *E. balteatus* follows a general trend for larger migrants with additional sex-specific female-weighted lower wing loading and enhanced flight capacity over male migrants of the same species (Menz *et al.*, 2019b; Doyle *et al.*, 2025).

A study on the transcriptomes of non-migratory summer and migratory autumn individuals of *E. balteatus* trapped in a high-altitude Pyrenean pass revealed over 1500 genes showing strong evidence for differential expression between these generations (Doyle *et al.*, 2022). Analyses of these genes revealed a remarkable range of roles in metabolism, muscle structure and function, hormonal regulation, immunity, stress resistance, flight and feeding behaviour, longevity, reproductive diapause, and sensory perception, all of which are key traits associated with migration and migratory behaviour (Doyle *et al.*, 2022). Several of these factors, particularly those involved in the circadian system, flight and hormonal control are shared with lepidopteran migrants. This suggests a common genetic basis to these traits and highlights the value of dipteran models for developing a comparative evolutionary framework of migration (Doyle *et al.*, 2022).

VI. GLOBAL DISTRIBUTION AND FLYWAYS

We found a global distribution of migratory behaviour in Diptera (Fig. 3). Records were recovered from all continents including, surprisingly Antarctica, with the calliphorid

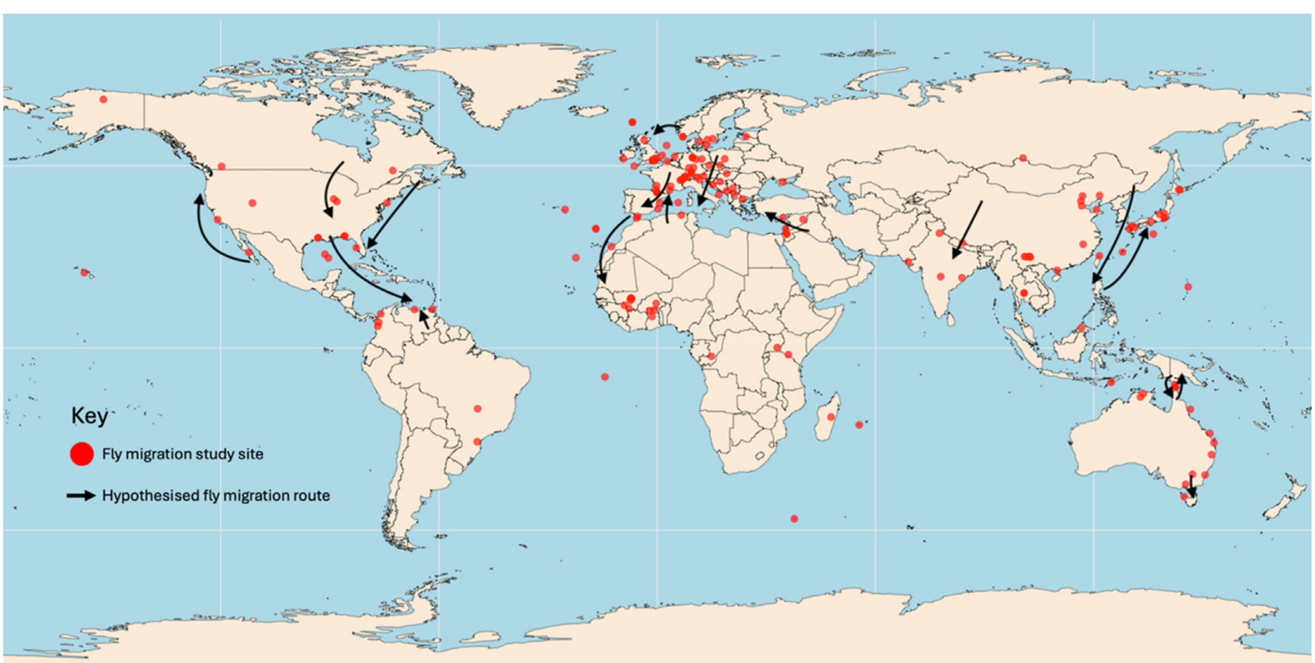

Fig. 3. The geographic distribution of dipteran migration studies and migratory flyways. Red dots represent locations of the dipteran migration studies identified in this review. Black arrows represent hypothesised migration routes based on known migrations from the published literature. These arrows represent likely broad fronts of movement and may be further influenced by geography, innate compass senses, and wind patterns.

Calliphora croceipalpis identified as a likely migrant to the sub-Antarctic Marion Island, 1700 km from South Africa, the closest non-snow-covered landmass (Chown & Language, 1994). The data point to a bias of European migration records, which make up 49% of publications, followed by Asia (13%), North America, Africa, and Australasia (all 10%) (Fig. 3). Location-specific information on the corridors used by these migrants is of key importance for future research, especially given the highly diverse ecological roles of Diptera. Below, we focus on each geographic region where fly migration is known to occur and on routes taken, which we refer to as 'flyways' in recognition of the geographic, ecological and climatic features that constrain movement to particular pathways. However, we recognise that much work is required to characterise these routes fully and they remain only hypotheses based on known migrations from the published literature.

(1) Eastern and western seaboard flyways of North America

On the eastern seaboard of North America, southward migration of Diptera during the autumn was recorded multiple times between 1915 and 1926, with calliphorids (*Cochlyomia macellaria*, *Calliphora vicina*, *Phormia regina*), muscids (*Stomoxys calcitrans*) and syrphids (*Eristalis tenax*) reported moving south in their 'thousands' (Shannon, 1926, p. 202). No further records have been published since then, and the status of these movements remains currently unknown (Menz, Brown & Wotton, 2019a). However, recent isotopic studies on the syrphid *Eupeodes americana* suggest that these flies can travel up to 3000 km from Canada to Alabama, indicating that a flyway down the eastern part of North America may still be well-utilised by migratory Diptera (Clem, Hobson & Harmon-Threatt, 2023) along with other migratory insects (Howard & Davis, 2009; Reppert & de Roode, 2018; Wikelski *et al.*, 2006; Hallworth *et al.*, 2018). By contrast, since the observations of Shannon (1926), only one migratory movement has been identified on the western seaboard, a northward movement of presumed *Eupeodes* sp. (Syrphidae) numbering in the hundreds of thousands in just half an hour, recorded on the west coast of California in April 2017 (Menz *et al.*, 2019a). It is likely that migratory Diptera regularly move north in the springtime and southwards in the autumn to exploit seasonal resources in North America. Citizen science data for *Eupeodes* (Syrphidae) shows that these flies move from lower latitudes during the winter months to higher latitudes during the springtime, suggesting seasonal long-distance movements along this flyway (Menz *et al.*, 2019a).

(2) Cross Caribbean flyway

Vast quantities of migratory insects including 17 families of Diptera have been recorded flying south in the autumn through the Portachuelo Pass, Venezuela (Beebe, 1951), along with many migratory bird species (Sainz-Borgo, Miranda & Lentino, 2020). The Portachuelo Pass runs north–south and opens towards the Caribbean Sea, collecting any insects flying across the ocean. In the late 1940s, insect migration was so plentiful that researchers had to wear glasses to protect their eyes from the swarms (Beebe, 1951). Although no insect-related studies have occurred at the Portachuelo Pass since then, more recent studies have recorded a variety of migratory Diptera (26 families) alighting on ships and oil rigs in the centre of the Gulf of Mexico, indicating that dipteran migration may occur across the Caribbean Sea (Keaster *et al.*, 1996; Sparks *et al.*, 1986).

(3) Western European flyway

Diptera migration has been best studied along the Western European flyway, although even here information remains sparse and restricted to just a few key sites. Long-term, whole-assemblage studies have been performed on migratory Diptera using suction traps in the UK, and mountain bottleneck studies in Germany, the French/Swiss Alps, the Pyrenees, and the Czech Republic (Aubert, Aubert & Goeldlin, 1976; Chapman *et al.*, 2004; Gatter *et al.*, 2020; Hlaváček, Lučan & Hadrava, 2022; Lack & Lack, 1951; Snow & Ross, 1952; Williams *et al.*, 1956; Hawkes *et al.*, 2024), and there have been many observations of migratory Diptera made from locations in the far north such as Norway and the North Sea, as well as south to the tip of Gibraltar (Ebejer & Bensusan, 2010; Hardy & Cheng, 1986; Jensen, 2001; Nielsen, Andreassen & Leendertse, 2010). A four-year study at a Pyrenean mountain pass in the autumn revealed 12 families of Diptera migrating south (Hawkes *et al.*, 2024). Radar and flight simulator studies have revealed directional movements of migratory Diptera, detailing a SSW bias in their autumnal movements (Chapman *et al.*, 2010; Gao *et al.*, 2020a; Massy *et al.*, 2024). This suggests that migratory Diptera found in Western Europe in the Autumn will be funnelled down into the Iberian Peninsula from large swathes of Europe, before potentially crossing into northern Africa *via* the straits of Gibraltar (Ebejer & Bensusan, 2010).

The majority of migration studies on Diptera have been performed in the autumn, but hints at their springtime routes are available. Large numbers of migratory Syrphidae have been found in the dunes in Gibraltar during the springtime, having just crossed the straits from Africa, a crossing well known for the large number of birds migrating between the continents (Ebejer & Bensusan, 2010). In 2022, large numbers of migratory Diptera, primarily Syrphidae, were found washed up on a beach in SW France, with wind analyses suggesting they were moving north over the Mediterranean before drowning due to a storm (Fisler & Marcacci, 2022). In the same year, large numbers of Syrphidae arrived on the Isles of Scilly, UK, with wind analysis suggesting that they took off over 200 km away in western France (Hawkes *et al.*, 2022b). *Culicoides obsoletus* (Ceratopogonidae) fly populations, which spread bluetongue and Schmallenberg viruses, were found to have high levels of gene flow and no genetic structuring at the scale of France during the springtime, suggesting movement during this period (Mignotte *et al.*, 2021). Further illumination of the routes may come from ambitious studies such as MoveInEurope, which operates a series of radars across Western Europe, as well as monitoring the routes birds take to understand if they are migrating along with insects to ensure a food source during the journey (Haest *et al.*, 2024).

(4) Eastern European flyway

The best evidence for an Eastern European flyway is from springtime studies reporting millions of Diptera (15 families) moving from the Middle East to Cyprus over at least 105 km of ocean (Hawkes *et al.*, 2022a). Many bird species have been found to use this route too, a large number migrating from Eastern Africa before following the Middle Eastern coast (Pedersen, Thorup & Tøttrup, 2019). Linking of the fertile regions of the Middle East by migratory Diptera in the springtime likely has major importance to eastern European countries in terms of nutrient and pollen transfer (Doyle *et al.*, 2020; Hawkes *et al.*, 2022a; Satterfield *et al.*, 2020). During the Autumn, many migratory birds are known to utilise the Georgian corridor to migrate southwards (Verhelst, Jansen & Vansteelant, 2011). The Georgian corridor area, to the best of our knowledge, has not been studied for dipteran movements, but often insect flyways mirror those of birds suggesting it is a location worthy of further study.

(5) Himalayan flyway

The areas north of India and the Himalayas such as Siberia, Mongolia, western China, and Kazakhstan are extensively fertile, but only seasonally during the summer months (Shpedt *et al.*, 2019). Therefore, these represent locations migratory Diptera can use to exploit seasonal resources before returning to the Indian subcontinent during the winter months. Isotopic studies from dragonflies captured in the Maldives suggest that they originated in southern Siberia, signifying huge distances are covered by migratory insects using this flyway (Hobson *et al.*, 2012). The great geographic barrier of the Himalayas creates migratory bottlenecks as the migrating animals are directed through mountain passes because of the winds and topography (Gatter, 1980; Westmacott & Williams, 1954). Therefore, identification of these mountain pass bottlenecks could enable easier monitoring of migratory behaviour. A few have been identified but not systematically sampled, providing only indications of a long-distance movement of migratory Diptera. *Episyrphus balteatus* (Syrphidae) were recorded flying through a Nepalese pass at 3700 m altitude, while various other Syrphidae have been seen migrating through the Thorong La pass at 5416 m altitude (Gatter, 1980; Westmacott & Williams, 1954). While only a handful of studies on migratory Diptera exist from these locations, it is expected to be a highly fertile area for future study.

(6) African movements

The size and considerable variety of habitats within the African continent makes it likely there are a great deal of dipteran migration routes, although little is known about them. A recent study based on the normalised difference vegetation index (NDVI) showed that the most suitable overwintering habitat for European-summering painted lady (*Vanessa cardui*) butterflies is within the sub-Saharan Sahel region (Hu *et al.*, 2021) while field data and ecological niche modelling indicates the Afrotropical region (Talavera *et al.*, 2023). Migratory Syrphidae have been found crossing the Straits of Gibraltar during the springtime suggesting that insects from Africa do recolonise Europe on their return migration (Ebejer & Bensusan, 2010). NDVI analysis in the Middle East suggested that the numbers of migratory Diptera, like the painted lady butterflies, are also correlated with increased vegetation growth (Hawkes *et al.*, 2022a). Therefore, if Diptera follow similar patterns to these butterflies, they too may be crossing the Sahara to reach more favourable Sahel regions. While, to the best of our knowledge, no direct evidence is available for migratory Diptera moving this far, the Bedouin people living at the Bawiti oasis area of Egypt see large numbers of migratory flies moving south in the autumn and north in the spring each year (Mohammed Khozam, personal communication). South of this area, the Sahara Desert continues until the Sahel region of Sudan, the next suitable overwintering habitat for these insects. This suggests that European dipteran migrants may continue across the Sahara on their spring and autumn migrations, making their journeys even more remarkable, but this requires confirmation.

In West Africa in Mali, a total of 28 families of Diptera including Anthomyiidae and Calliphoridae have been recorded making seasonal back and forth movements at altitudes from 40 to 290 m (Florio *et al.*, 2020). Some of these species are likely long-distance migrants that crossed the Sahara, but as the study was primarily nocturnal (aerial traps were open from 17:00 to 07:30 h) it is possible that many diurnal dipteran migrants were missed. Other migration routes in Africa include the annual arrival of Simuliidae flies to the Volta River basin in West Africa from distant source areas with the onset of the migration season (Garms, Walsh & Davies, 1979). Wind patterns also move large quantities of mosquitoes around West Africa, with the West African monsoon winds enabling large numbers of dipteran migrants to exploit the seasonal resources created by the monsoon rains (Dao *et al.*, 2014; Huestis *et al.*, 2019; Parker *et al.*, 2005).

Eastern and southern Africa have even fewer studies than west Africa. However, there is some evidence of dipteran migrants (Glossinidae) arriving with the rains from long distances in Kenya (Brightwell *et al.*, 1997). This suggests that flies here too are utilising the regular seasonal patterns of monsoon winds to migrate, and it is likely that far more taxa are also using these meteorological conditions to exploit seasonal resources in the region (Funk *et al.*, 2016). Africa is an understudied region in terms of dipteran migration, but there is little doubt there are many migration routes yet to be discovered.

(7) East Asia to SE Asia

The East Asian Insect Flyway has recently been characterised by Hu *et al.* (2024) with a focus on migratory lepidopteran and planthopper pests. The flyway covers mainland Southeast Asia and the Philippines in the south, through East China and adjacent parts of Mongolia, to the Russian Far East and Japan in the north (Jia *et al.*, 2022; Liu *et al.*, 2019; Kurahashi, 1997; Nabeshima *et al.*, 2009). Dipteran migrants in this flyway have been identified by long-term studies on Beihuang, a small, isolated island in the Bohai Strait, NE China that included trapping, trajectory analysis, and intrinsic markers, and revealed that *E. balteatus* (Syrphidae) exhibit seasonal back and forth latitudinal movement, passing the island each year on long-distance migration (Jia *et al.*, 2022). Population genetics studies have also revealed that *Eupeodes corollae* (Syrphidae) shows little differentiation in its population across the whole of China, suggesting regular long-distance movements that maintain gene flow across the whole geographic area (Liu *et al.*, 2019). Migration to the Japanese islands from the Asian mainland may also be occurring regularly. Reports have been made of groups of *Calliphora nigribarbis* (Calliphoridae) flies arriving on southern Japan from the Korean peninsula, some 300 km to the NW during the autumn migration season (Kurahashi, 1997). Based on phylogenetic analysis of Japanese Encephalitis Virus (JEV) strains found in Japan, it has been determined that at least some strains originated in Vietnam and China's inland region, while others originated in Shanghai, China (Nabeshima *et al.*, 2009). It has been suggested that the mosquito vectors of this disease migrate to the area regularly, brought from SE Asia by a seasonal low-level jet stream during the rainy season [which also brings the brown leafhopper (*Laodelphax striatellus* - Hemiptera) to Japan] and on westerly winds from mainland China (Nabeshima *et al.*, 2009).

(8) Oceania

Like many areas, Australian migratory Diptera are poorly studied. A flyway of various species seems to exist between SE Asia and Northern Australia, especially between Papua New Guinea and Queensland across the Torres Strait. Mosquitoes are thought to enable the regular ingress of JEV into Australia from Papua New Guinea, utilising favourable winds (Ritchie & Rochester, 2001). Similar movements are known of *Culicoides* sp. (Ceratopogonidae) as vectors of diseases including Blue Tongue between Indonesia, Papua New Guinea and Queensland (Eagles *et al.*, 2014). Movements of *Melangyna* sp. (Syrphidae) also have been recorded across the Bass Strait between Tasmania and mainland Australia during the springtime (Hill, 2013), although given the size and climatic variability of the Australian continent, these SE Asia–Australia and Australia–Tasmania flyways are unlikely to be linked. A citizen science study of Syrphidae in Australia showed that there were major latitudinal movements throughout the year in four species (*Melangyna viridiceps*, *Simosyrphus grandicornis*, *Eristalinus punctulatus*, and *Eristalis tenax*), a behaviour suggestive of migration (Finch & Cook, 2020) however, further work is needed in Australia to reveal the true geographical range of movements of migratory Diptera. *Eristalis tenax* is a cosmopolitan species and appears in migration studies from Europe and North America and is found in Australia and New Zealand (Finch & Cook, 2020; Hawkes *et al.*, 2022a, 2024; Jia *et al.*, 2022; Shannon, 1926). The cosmopolitan distribution of these migrants could allow studies into the behaviour and genomics of the same species across multiple continents.

(9) Other potential flyways

Vast swathes of the globe are understudied in terms of migratory Diptera and there are undoubtedly more species and flyways to be discovered (Fig. 3). No records of Dipteran migration have been found from sub-equatorial South America. Given that the vast latitudinal difference covered by this landmass will give rise to many seasonal resources to exploit, conditions seem perfect for the presence of migratory Diptera. Similarly, southern Africa is understudied yet has great potential. One method for determining migratory flyways of Diptera is monitoring the routes of migratory birds or the systematic monitoring of insects at likely visible migration points in the landscape. For example, migratory globe-skimmer dragonflies (*Pantala flavescens*) migrate between India and Africa on monsoon winds (Anderson, 2009) and so smaller dipteran species may also be traversing the same immense distance to exploit the seasonally available conditions created by the monsoons. Genetic studies have revealed that species of Drosophilidae and Tephritidae found in East Africa have their origins in India, likely having been blown across on the seasonal winds (Jacquard *et al.*, 2013; Tsacas, 1984). Additionally, large numbers of *Chrysomya megacephala* (Calliphoridae) were recorded arriving on an island in the Maldives suggesting a similar journey to the globe-skimmer dragonflies (W.L. Hawkes, personal observations). Interestingly, also on the Maldives, parasitic *Forcipomyia* midges were recorded clinging to the wings of migratory globe-skimmer dragonflies that had presumably just arrived from India (W.L. Hawkes, personal observations), an example of phoretic migration by these dragonfly-riding flies. These strands of information on migratory Diptera in these areas provide exciting opportunities for further research.

VII. ECOLOGICAL ROLES

Compared to migratory insects of other taxa, the variety of ecological roles played by the Diptera is unparalleled. For example, the Odonata are found around freshwater habitats with both predatory larvae and adults while the Lepidoptera mostly have terrestrial plant feeding larvae and are pollinators as adults. By contrast, the Diptera occupy an extraordinary breadth of terrestrial and aquatic habits associated with an impressive range of ecological roles, including as pollinators, decomposers, predators, parasites and pests, while exhibiting a highly diverse range of feeding habits. Diptera are recognised as vital in maintaining ecosystems and as ecosystem engineers and keystone species in many habitats (Adler & Courtney, 2019). We identified a diverse range of dipteran migrants numbering 592 species from 60 families. The ecological roles of these species were determined from a variety of sources including guidebooks and scientific publications (Table S3), revealing that 62% of these species were pollinators, 35% were decomposers, 18% were pests, 16% were disease vectors, 10% pest controllers, and all played a role in the transfer of nutrients. The total sum is over 100% as individual species can play multiple ecological roles. Understanding the ecological roles of migratory Diptera is important when considering the impacts of these movements of flies globally.

(1) Pollinators

An estimated 62% of identified Dipteran migrants function as pollinators. Rader *et al.* (2020) found that Diptera visited 72% of major food crops. Six families of flies visited more than 12 major food crops, Syrphidae, Calliphoridae, Muscidae, Sarcophagidae, Tachinidae, and Bombyliidae, and all included species that are known migrants. Amongst these families, the Syrphidae and the Calliphoridae were the most common visitors (Rader *et al.*, 2020). The Syrphidae alone have been found to pollinate 52% of major food crop plants globally with an estimated worth of around US$300 billion per year (Doyle *et al.*, 2020; Rader *et al.*, 2020).

Migratory pollinators may be exceptionally important to global ecosystems because, unlike more sedentary pollinator species (like most bees) they transport pollen great distances and can link geographically isolated plant populations (Doyle *et al.*, 2020; Lysenkov, 2009; Meyer, Jauker & Steffen-Dewenter, 2009; Rader *et al.*, 2011). Evidence for long-distance transfer of pollen was found for individual *E. tenax* (Syrphidae) and *C. vicina* (Calliphoridae), caught after flying at least 105 km across the eastern Mediterranean from the Middle East to Cyprus with Bug Orchid (*Anacamptis coriophora*) pollen attached to their faces (Hawkes *et al.*, 2022a). Further pollen analysis by DNA barcoding revealed that these same *E. tenax* flies were carrying at least seven other species of pollen upon their bodies (W. L. Hawkes & T. Doyle, unpublished data) while data from migratory *E. balteatus* and *E. corollae* caught in the Alps revealed average pollen loads of 10.5 grains per fly (Wotton *et al.*, 2019). Pollen can remain viable for many days (Gibernau *et al.*, 2003) and these insects are capable of moving hundreds of kilometres in a matter of hours with wind assistance (Hawkes *et al.*, 2022b) suggesting that viable pollen can be transferred great distances. Migratory pollinators can be very numerous; it has been estimated that just two species of Syrphidae could transport 3–8 billion pollen grains into southern Britain from the near continent each year, and 3–19 billion pollen grains out to the continent in the Autumn (Wotton *et al.*, 2019). Such movements likely have highly significant consequences for long-range gene flow mediated by insect migration. For example, the movement of pollen may allow increased gene flow between populations which in turn may increase the resistance of plants to inbreeding depression, increase population survival and maintain the health of isolated populations (Luo, Xia & Lu, 2019; Pérez-Bañón *et al.*, 2003). Migratory pollinators may also allow for adaptions by plant populations to counter a warming climate by spreading alleles favourable for disease resistance or drought (Luo *et al.*, 2019; Pérez-Bañón *et al.*, 2003). Small islands without the ability to support populations of sedentary pollinators may especially benefit from migratory dipteran pollinators. For example, in the Columbretes archipelago of Spain the migratory syrphid *E. tenax* is known to be the major pollinator species, alongside the migratory calliphorid *Lucillia sericata* (Pérez-Bañón, Petanidou & Marcos-García, 2007).

(2) Decomposers

Migratory animals rely on arriving in areas with suitable seasonal resources (Dingle, 2014). Many species of migratory Diptera are decomposers (e.g. Calliphoridae and eristaline Syrphidae), taking organic matter from a dead organism or an organism's waste and breaking it down into simple organic substances which can subsequently be taken up by other organisms (Losey & Vaughan, 2006). Studies have revealed that migratory Diptera with a major role in decomposition comprise a significant part of the entire migratory assemblage (16% in Cyprus, 33.6% in Pyrenees) (Hawkes *et al.*, 2022a, 2024). From Table S3 we estimate that of all known migrant Diptera, 35% play a role in decomposition.

Many dipteran migrant decomposers feed on decaying plant or fungal matter or animal waste. Migratory Calliphoridae such as *L. sericata* (Diakova *et al.*, 2018) and the *C. vicina* group lay their eggs on carrion, upon which their offspring feed (Anderson, 2011). These carrion feeders are known to fly great distances (Hawkes *et al.*, 2022a) and some of their populations are considered panmictic, suggesting high levels of migration (Diakova *et al.*, 2018), therefore nutrients taken from carrion by their larvae can be redistributed across large areas. The Muscidae provide additional important examples. For example, *Musca domestica* larvae are coprophagous and saprophagous, and prefer to live in areas with high microbial and organic contamination (Čičková *et al.*, 2012) where they are efficient decomposers. They therefore aid the biodegradation of organic waste, especially within synanthropic conditions (in association with and benefitting from human activities) (Čičková *et al.*, 2012). In ideal conditions, larvae produced by 50 *Musca domestica* flies (25,000 eggs) can decompose up to 444 kg of pig slurry, transforming it into organic compost with excellent agronomic potential (Čičková *et al.*, 2012). The migratory eristaline hoverfly *E. tenax* is thought to play similar decomposition roles with great potential for aiding waste recycling (Francuski *et al.*, 2014; Ecodiptera, 2009). The impacts of migratory Diptera on decomposition efforts globally have not been quantified, but given their abundance in migratory assemblages, could be large. Strategies involving the planting of wildflowers and provision of other habitats for migratory Diptera near areas where decomposition is needed (livestock slurry pits for example) could allow maximisation of the decompositional roles of migratory Diptera.

(3) Pests

The intensification of agriculture increasingly means there are vast swathes of land dedicated to monocultures globally (Meyer & Turner, 1992). Migratory species need to be able to find resources, and the species that have evolved to use abundant crops or livestock as a food source have been the most successful (Guo *et al.*, 2020). Monocultures of crops have led to local simplification of insect biodiversity, reducing populations of their natural enemies, in turn creating conditions suitable for agricultural pests to flourish (Sánchez-Bayo & Wyckhuys, 2019). Many migratory Diptera are classed as agricultural pests, from Table S3 we estimate this to be around 18% of all known dipteran migrants. For example, some migratory species of Chloropidae, such as *Oscinella frit*, are pests of various cereals, grasses, and spring-sown maize (El-Wakeil & Volkmar, 2011; Southwood & Jepson, 1962). In spring 2019, over 15 million *Delia platura* (Anthomyiidae) were estimated to be migrating long distances (minimum 105 km) from the Middle East to Cyprus; this species is a generalist crop pest of nearly 50 plant species (Guerra *et al.*, 2017; Hawkes *et al.*, 2022a). This was the first record of this species migrating in such large numbers, suggesting either an increase in its abundance or in the prevalence of its migratory behaviour. Species such as the stable fly *S. calicitrans* (Muscidae) are costly pests of livestock (particularly cattle) (Campbell, Boxler & Adams, 2002; Gerry, 2007), the adult flies feeding on the blood of mammals to provide a protein source before laying their eggs (Bishopp, 1913). These flies seasonally recolonise dairy farms (Beresford & Sutcliffe, 2009) and can fly at least 225 km based on mark–release–recapture experiments (Hogsette & Ruff, 1985). *Cochliomyia homininvorax* (Calliphoridae) is a well-known migrant and a major pest of livestock. Its larvae cause myiasis, burrowing into the flesh of mammals to feed and develop (Costa-Júnior *et al.*, 2019). Methods for controlling these species often include use of pesticides, however rates of pesticide resistance in migratory organisms have been found to be high (Hemingway *et al.*, 1997; Raymond & Pasteur, 1996), underlining the need for a greater understanding of the life histories and movement patterns of migratory species to inform management.

(4) Disease vectors

One of the most important impacts that migratory Diptera have is as vectors of disease, with 16% of identified dipteran migrants thought to play this role. Of all the migratory dipteran families, the mosquitoes (Culicidae) have been the best studied in this regard. Mosquitoes are known vectors of diseases that kill over half a million people globally every year (Bueno-Marí *et al.*, 2022). *Anopheles coluzzii* mosquitoes which are the primary malaria vector have been shown to engage in windborne migration above Africa, travelling up to 300 km in 9 h (Huestis *et al.*, 2019). Of other families, the blackfly *Simulium damosum* (Simuliidae) is capable of moving hundreds of kilometres each year on monsoon winds across west Africa, spreading a nematode (*Onchocerca volvulus*) that causes river blindness (Baker *et al.*, 1990), and migratory *Culicoides* sp. (Ceratopgonidae) are known to aid the seasonal recurrence of blue tongue disease in Israel each year (Braverman & Chechik, 1993). Within the Muscidae, the stable fly *S. calcitrans* is thought to be able to transfer food-associated human pathogens from agricultural to urban areas (Mramba, Broce & Zurek, 2007), as well as directly transmitting wildlife diseases (Mihok & Clausen, 1996). Some migratory Diptera are involved in the transmission of plant diseases. For example, the bean seed fly *D. platura* (Anthomyiidae) has been recently discovered to be a major vector of soft rot bacteria (Pasanen, 2020). Another understudied research area is the role that migratory Syrphidae may play in the transfer of diseases that affect honeybees (*Apis mellifera*) and other bee species, such as deformed wing virus, to previously unaffected populations (Fischer *et al.*, 2006). However, although the presence of this disease has been identified within migratory *E. tenax*, there was no evidence of viral replication within *E. tenax* or evidence for whether the disease can be actively passed on to the bees (Fischer *et al.*, 2006).

Mosquito-transmitted diseases are generally a major problem within warmer, more tropical, areas where the Diptera involved in vectoring these diseases (e.g. mosquitoes, tsetse flies, and Simuliidae) can occur in abundance (Huestis *et al.*, 2019). With global warming, it is predicted that an additional 4.7 billion people will be affected by these diseases by 2070 compared to 1999 numbers (Colón-González *et al.*, 2021). Rising temperatures are predicted to increase the suitability of temperate locations for the survival of these disease vectors. The range expansion of these diseases could be most problematic in areas where the human population is immunologically naïve, or healthcare systems are unprepared (Colón-González *et al.*, 2021). The migratory behaviour of these dipteran vectors increases the complexity of combatting such diseases as a new influx of pathogens is introduced each year with the migratory insects' arrival (e.g. Lebl *et al.*, 2015; Riad *et al.*, 2017). This necessitates the development of management plans which consider the long-distance movement of the vectors. Currently, many insect vectors of disease are understudied in terms of their migratory behaviour, and targeted research on their movement patterns could have significant impacts for human health.

(5) Pest controllers

Many arthropods are pests that cause damage to agricultural crops, and many migratory Diptera are predators upon these pests at some stage in their life histories (Courtney *et al.*, 2009). We found that 10% of all migratory Diptera play the role of pest controllers. These pest controllers include many representatives from the Syrphidae, such as the aphidophagous *E. balteatus* and *E. corollae* (Wotton *et al.*, 2019) as well as from the Calliphoridae, such as *Stomorhina lunata* which feeds upon locust larvae (Greathead, 1962). Tachinidae are also known to be useful pest controllers as they lay eggs in a variety of insect larvae including those of the Lepidoptera, Coleoptera, Hemiptera, and Symphyta. For example, the migratory *Tachina fera* (Tachinidae) has been used to control populations of the gypsy moth *Lymantria dispar* in forest environments (Davis, 2013). It is presumed that most migrant species are generalists or at least target highly abundant prey sources. As a result of increased agricultural land coverage, species that are classed as pests have generally become more dominant in recent times (Guo *et al.*, 2020). Because of this, the migratory Diptera that prey on these pests are increasingly important, especially given the rise of pesticide resistance and the other ecological benefits that migratory Diptera bring to agricultural landscapes (Doyle *et al.*, 2020; Hemingway *et al.*, 1997; Raymond & Pasteur, 1996).

Of the migratory Diptera, Syrphidae are best studied regarding pest control (Rojo *et al.*, 2003). Aphidophagous Syrphidae are common migrants across all continents except Antarctica, making the total impact in terms of pest control by migratory Syrphidae likely to be huge. Many migratory species such as the abundant *E. balteatus* and *E. corollae* feed on aphids as larvae and therefore are beneficial to agriculture. Indeed, both species are available commercially as biological control agents for use in glasshouses (Moerkens *et al.*, 2021; Pineda & Marcos-García, 2008). The larvae of *E. balteatus* and *E. corollae* are voracious predators and it has been estimated that the progeny of flies migrating to southern England during the springtime consume up to 10 trillion aphids each year (Wotton *et al.*, 2019). However, the contribution to biological control by all migratory Syrphidae is likely to be much greater, as the impact of other immigrations or generations produced by other migratory species is yet to be calculated.

(6) Nutrient transfer

It is thought that insect migration represents the most important animal movement annually in terrestrial ecosystems (Hu *et al.*, 2016). As migratory Diptera are multi-generational migrants, when they reach a suitable area, they lay their eggs and die (Chapman *et al.*, 2015), hence, all (100%) of these insects have a function in nutrient transport between geographically distant ecosystems *via* carcass deposition (Hu *et al.*, 2016; Satterfield *et al.*, 2020). The dry body mass of a migratory fly is typically 10% nitrogen and 1% phosphorus – elements which are limiting to plant growth (Elser *et al.*, 2000). Therefore, these insects represent a potential source of nutrient influx for ecosystems. Few studies have documented the influence of nutrient transfer by migratory insects, and fewer still have focussed on the Diptera. Wotton *et al.* (2019) estimated that the 4 billion *E. balteatus* and *E. corollae* Syrphidae migrating above southern England each year comprise 80 tons of biomass and will deposit 2500 kg of nitrogen and 250 kg of phosphorus a considerable distance from their source. The entire migratory assemblage moving annually across southern England has been estimated at 3200 tons, 7.7 times the 415 tons of biomass of migrating songbirds, highlighting the huge importance of migratory insects to nutrient transfer (Hu *et al.*, 2016). Migratory Diptera are known to be abundant in migratory assemblages, and extrapolating the values calculated for the Syrphidae to all other migrant Diptera, the movement of nutrients each year is likely to be immense.

However, far more research is needed, particularly for high-latitude environments, where very few organisms can survive the winter months and where the annual, dependable influx of migratory Diptera may provide vital nutrients for the growth and blooming of vegetation. Animals of higher trophic levels that rely on insects as food, such as birds (Tallamy & Shriver, 2021), may depend on the springtime influx of migratory Diptera each year to provide food for their young or to fuel their own migrations. Finally, a large percentage of migratory Diptera may regularly end up drowning in the sea. Migrating Diptera are often trapped on ships far out in the ocean, for example, *Calliphora nigribarbis* and *Aldrichina grahami* (Calliphoridae) were caught 300–450 km off Japan in the Pacific Ocean (Kurahashi, 1991). While some flies may eventually reach shore, many more likely drown in the ocean due to exhaustion or inclement weather conditions. In 2022, large numbers of Syrphidae were washed up on a beach in southwestern France after being caught in a storm and drowning (Fisler & Marcacci, 2022). These perished flies may provide additional nutrients for marine ecosystems (Hawkes *et al.*, 2022a).

VIII. ANTHROPOGENIC STRESSORS ON MIGRATORY DIPTERA

The natural world is under intense pressure from anthropogenically induced changes with migratory species under a range of threats including climate change, habitat loss, and increased pollution (Cooke *et al.*, 2024). In many insect taxa both resident and migratory species have undergone precipitous population declines: one study monitoring flying insect biomass in Germany revealed a 76% decline over 27 years (Hallmann *et al.*, 2021). Similarly, in the UK the number of insect impacts on car numberplates reduced by 64% in the 18 years since 2004 (Ball *et al.*, 2022). When compared to their sedentary counterparts, however, migratory Diptera that have wide habitat ranges and multiple generations throughout the year are thought to be more resilient to the effects of climate change (Biesmeijer *et al.*, 2006). Even so, the few studies documenting declines in migratory dipteran populations are still damning. For example, in the last 50 years the number of aphidophagous Syrphidae migrating autumnally through Randecker Maar in the Schwäbische Alb uplands of southwest Germany has declined by 97% (Gatter *et al.*, 2020). Such declines may have drastic impacts. For example, North American insectivorous bird numbers have dropped by an estimated 2.9 billion in the last 50 years, compared to non-insectivorous birds whose numbers have increased by 26.2 million individuals (Tallamy & Shriver, 2021). A recent European study on Syrphidae has predicted the loss of some sedentary species from lowland areas and gains in alpine locations (Miličić, Vujić & Cardoso, 2018). The majority of agriculture is found in lowland regions and so the loss of these insect pollinators could negatively impact crop yields. Migratory species of Syrphidae have high reproductive rates and mobility and, like other insect migrants (Baker, Venugopal & Lamp, 2015; Bale & Hayward, 2010; Zeng *et al.*, 2020), could be capable of adapting to climate change, making them particularly important for counteracting crop damage caused by poleward shifts in pests such as aphids (Bebber, Ramotowski & Gurr, 2013).

While insect population declines are due to a variety of factors, a prominent role is given to climate change and habitat loss (Goulson, 2019). Global temperatures are likely due to rise between 2 and 4.9 °C above pre-industrial levels by 2100 (Raftery *et al.*, 2017). Increasing temperatures therefore could result in higher latitude countries receiving more dipteran migrants. Data on migratory Lepidoptera abundance and temperature spanning 113 years have shown that these migrants have become more abundant in the UK with increasing temperatures (Sparks *et al.*, 2007). This is thought to be in part because of increased aridity in southern Europe encouraging northward migration (Sparks *et al.*, 2007), something that is likely mirrored by dipteran migrants. Increasing temperatures at higher latitudes is also increasing the suitability for overwintering by migrants. This could lead to the loss or rebalancing of migratory behaviour in many dipteran species which tend to be partial migrants (Menz *et al.*, 2019b). As a result, the ecological benefits of the migratory behaviour of Diptera detailed above may also be lost. Interestingly, the presence of partial migration, where part of the population remains in the breeding area instead of migrating, in many species of migratory insect may lead to some resilience to climate shifts (Menz *et al.*, 2019b). For example, some individuals of the migratory syrphid *E. balteatus* overwinter in parts of central Europe (Luder, Knop & Menz, 2018; Odermatt, Frommen & Menz, 2017; Raymond *et al.*, 2014), and can do so at all life stages: eggs, larvae, pupae and adults (Raymond *et al.*, 2014). These overwintering animals provide critical early-season control of aphids colonising crops before migratory individuals have arrived (Raymond *et al.*, 2014). With warming climates, we may see an increase in the proportion of individuals and species overwintering and forgoing migration.

Increasing temperatures due to climate breakdown could also lead to phenological asynchronies between taxa. The timing of dipteran migration may be linked to temperature as seen in some migratory butterflies such as the red admiral (*Vanessa atalanta*) (Sparks, Roy & Dennis, 2005); the phenology of first sighting of Syrphidae in the UK has advanced earlier in the year as the planet warms (Hassall, Owen & Gilbert, 2017). Myriad other organisms may rely upon (or are relied upon by) the arrival of dipteran migrants, including passerine birds, or wildflowers that provide a vital food source for migrating Diptera and may themselves rely on Diptera for pollination services (Hawkes *et al.*, 2022a; Losey & Vaughan, 2006). If these organisms use day length rather than temperature to entrain their activities, then asynchrony may result, with potentially disastrous impacts (Mayor *et al.*, 2017). A literature review on the ecological impacts of temperature-mediated trophic asynchrony revealed a dearth of studies (Samplonius *et al.*, 2021), with those that do exist biased towards terrestrial higher trophic secondary consumer taxa such as birds, and the northern hemisphere (Samplonius *et al.*, 2021). Far more research is needed to inform conservation efforts and to understand the possible consequences of phenological change.

The range of many wind-borne dipteran migrants is expanding in response to increases in temperature, as seen for some *Aedes* mosquitoes, which are important vectors of diseases such as malaria. Wind patterns transporting mosquitoes to high-altitude settlements in the Himalayan region used to pose no threat to humans as cold temperatures kill mosquitoes (Dhimal *et al.*, 2021). However, with global warming, mosquitoes can now survive in these regions and transmit diseases such as malaria, thus posing a serious threat to these communities (Dhimal *et al.*, 2021). Increasing temperatures globally mean that higher latitude countries are now at threat from mosquito-vectored diseases due to better conditions for mosquito survival (Agyekum *et al.*, 2021). The response of disease vectors to changes in climatic conditions has significant consequences for predicting and managing outbreaks of disease.

Increased extreme weather events such as droughts or extended periods of rainfall due to climate breakdown also are likely to have negative impacts on migratory Diptera populations due to changes in habitat suitability. Increased drought may cause vegetation to wither prematurely and the eggs of Diptera to dry out and become unviable. Similarly, increased rainfall may be detrimental to Diptera larvae that develop underground, as they can drown in waterlogged soil. Droughts and the loss of moist habitats can lead to a reduction in the availability of suitable breeding sites for many saprophagous species that have semi-aquatic larvae, such as the syrphid *E. tenax*.

Finally, increased CO_2 levels have been shown to reduce the amount of nitrogen in plant leaves by 10–30%. To compensate for reduced nitrogen availability, herbivory levels by crop pests (including many migratory Diptera) may increase by 20–90% (Kinney *et al.*, 1997; Roth & Lindroth, 1994, 1995), potentially leading to increased crop damage. Very little is known about the response of migratory Diptera to climate change. Research into the ecological roles, range shifts, and declines of these hugely important species is needed so that their impacts can be understood, encouraged or mitigated, particularly in the context of ecosystem and human health.

IX. CONCLUSIONS

(1) Our analyses of the literature on migrant Diptera reveal a highly diverse set of 592 suspected migrant species from 60 families, many of which appear to be highly abundant, and to migrate in huge numbers.
(2) Dipteran migrants, compared to other migratory insect orders, play an unsurpassed range of ecological roles, marking them out as a major contributing force to the functioning of terrestrial and aquatic ecosystems and the economy.
(3) Compared to other groups, very little is known about migratory Diptera and for many of the migratory families only a single study related to migration was found. We recommend a greater focus on the taxonomic diversity of dipteran migrants in future studies. This will help to understand the ecological roles of these insects as they connect distant landscapes.
(4) We recommend further study using techniques such as monitoring and trapping in migration bottlenecks, stable isotope and pollen analysis, trajectory analysis, flight simulators and flight mills, and NDVI measurements, along with emerging approaches such as radar networks, that can be used to infer behaviour, assemblages, origins, destinations, headings and numbers of mass movements of dipteran migrants.
(5) Many anthropogenically beneficial dipteran migrants are under threat from climate change and other anthropogenic impacts. It is possible that many migratory flies and their behaviour could disappear without being documented unless action is taken.
(6) To conserve these vitally important taxa, it will not be enough to protect or restore habitat at single locations; the entire migratory route must be capable of sustaining these insects, as for other migratory species (Runge *et al.*, 2014). Refocusing agricultural, rewilding and conservation practices to ensure landscape connectivity could have the greatest impacts. Understanding the migratory cycles and pathways of these ecologically important species will be key to future conservation measures.

X. ACKNOWLEDGEMENTS

We would like to thank Toby Doyle for assistance while writing this manuscript. W. L. H. would like to thank Sarah Hawkes, Tim Hawkes, Renn Hawkes, Oona Hawkes, and Eira Hawkes for helping and lending their enthusiasm to this project. Final thanks must go to the migratory flies themselves, without whom this manuscript would not exist.

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XII. SUPPORTING INFORMATION

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

Table S1. Comparison of migratory criteria for Diptera used herein with those used by Chowdhury *et al.* (2021).
Table S2. Evidence for fulfilling migratory criteria in each of the dipteran families.
Table S3. Evidence for migratory behaviour and their ecological roles in each of the 592 known dipteran migrant species.

(*Received 5 March 2024; revised 13 March 2025; accepted 19 March 2025; published online 1 April 2025*)