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Research

Huge spring migrations of insects from the Middle East to Europe: quantifying the migratory assemblage and ecosystem services

Will L. S. Hawkes, Edward Walliker, Boya Gao, Olivia Forster, Katharine Lacey, Toby Doyle, Richard Massy, Nicholas W. Roberts, Don R. Reynolds, Özge Özden, Jason W. Chapman and Karl R. Wotton

W. L. S. Hawkes, E. Walliker, B. Gao, O. Forster, K. Lacey, T. Doyle, R. Massy, J. W. Chapman and K. R. Wotton (https://orcid.org/0000-0002-8672-9948) ✉ (k.r.wotton@exeter.ac.uk), Centre for Ecology and Conservation, Univ. of Exeter, Cornwall Campus, Penryn, UK. BG and JWC also at: Dept of Entomology, Nanjing Agricultural Univ., Nanjing, China. – N. W. Roberts, School of Biological Sciences, Univ. of Bristol, Bristol, UK. – D. R. Reynolds, Natural Resources Inst., Univ. of Greenwich, Chatham, Kent, UK and Rothamsted Research, Harpenden, Hertfordshire, UK. – Ö. Özden, Faculty of Agriculture, Near East Univ., North Cyprus, UK and Cyprus Herbarium and Natural History Museum, Near East Univ., North Cyprus, UK. JWC, Environment and Sustainability Inst., Univ. of Exeter, Cornwall Campus, Penryn, UK.

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Migratory insects are a key component of terrestrial ecosystems, but understanding their full contribution is challenging as they are difficult to track, and migration often takes place at high altitude. Migration hotspots offer an exceptional opportunity to study these otherwise indiscernible movements as migration can be visible at ground level; however these events are often also ephemeral and reported only from chance encounters. It is therefore often difficult to fully characterise the range and number of species involved, the drivers of migration or to appreciate the potential interactions and ecological roles of the migrants. Here we pursue field evidence suggesting that the Karpaz peninsula in northeast Cyprus is a suitable location to systematically collect data on migratory insects. In the spring of 2019, using a combination of timed-counts, migration-camera traps and netting we documented over 39 million day-flying insects from eight orders arriving on Cyprus at rates of up to 5900 insects m^{-1} min^{-1}. Mass arrivals were correlated with higher temperatures and easterly winds. Wind direction and normalised vegetation difference index (NDVI) data suggest that these insects had their natal origins in locations including Syria, Iraq and Saudi Arabia. It is estimated that many billions of insects left the coast of the Middle East heading west into Europe during the study period. While the migrant assemblage was diverse, Diptera were by far the most numerous insect order (86%) followed by Lepidoptera (10%). These migrating insects play a range of vital ecological roles including cross-continental pollination and the transfer of important nutrients. We believe that the very infrequently explored processes described in this manuscript have important consequences for ecosystems in the destinations of these migratory insects across Europe.

Keywords: eastern Mediterranean, ecological impacts, insect migration flyway, migration rates, movement ecology, source area NDVI

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Introduction

Insects are the most numerous terrestrial migrants, far surpassing vertebrates in terms of biomass and abundance (Chapman et al. 2015, Hu et al. 2016). Insects are thought to migrate primarily to exploit seasonal resources in order to increase reproductive output and/or escape habitat deterioration, e.g. due to temperature, food quality or disease risk (Dingle 2014, Chapman et al. 2015). Spring and summer in northern Europe are associated with huge influxes of migratory insects as habitats become temporarily suitable to support reproduction. Butterflies such as the painted lady *Vanessa cardui* (Stefanescu et al. 2013), and red admiral *Vanessa atalanta* (Stefanescu 2001), the silver Y moth *Autographa gamma* (Chapman et al. 2008, 2012), migratory hoverflies (Wotton et al. 2019) and some dragonflies (Wikelski et al. 2006) are known to exploit these temporal resources. Life histories such as theirs appear to be associated with high reproductive advantages (Chapman et al. 2012, Wotton et al. 2019) and migrants are often among the most numerous insects in various natural and agro-ecosystems (Chapman et al. 2015).

Migratory insects carry out a huge range of ecological roles varying from pest controllers and pollinators, as well as activities negative to humans such as crop pests and vectors of disease (Satterfield et al. 2020). In addition, they also transport essential nutrients and propagules between ecosystems (Landry and Parrott 2016) or act as food for insectivorous species (Wotton et al. 2019, Satterfield et al. 2020). Identifying the composition of migratory bioflows is key to understanding their impact and studies have utilised a number of approaches including aerial netting (Chapman et al. 2004), capture and identification in migratory hotspots (Lack and Lack 1951, Aubert et al. 1976, Gatter et al. 2020) and radar techniques to target particular species (Chapman et al. 2012, Wotton et al. 2019, Gao et al. 2020). In general, these studies have occurred at higher latitudes. Less data exists from lower latitudes where migratory insects may overwinter or continue to breed. Large spring migrations have seldom been observed in western Europe, perhaps because of the inaccessibility, due to heavy snow, of migration hotspots in mountainous passes which see migration in the autumn such as the Alps and Pyrenees (Lack and Lack 1951, Aubert et al. 1976) or the invisibility of migration over large areas of land. There are exceptions, for example in May 2009 the arrival of millions of painted lady butterflies reaching the UK (Stefanescu et al. 2013). However, as these are rare events it has been difficult to build up a detailed picture of the phenomenon of spring insect migration.

One potential incoming route to Europe, for the annual repopulation, is from the Middle Eastern region which serves as a flyway for some passerine migrants from Africa in the spring (Pedersen et al. 2019). Interestingly, after flying from Africa into the Middle East via Saudi Arabia, some passerine migrants such as red-backed shrikes change direction to fly via Cyprus (Tøttrup et al. 2012). This suggests that the island may form a stepping stone into western Europe and allow migrants to avoid the high Taurus Mountains in Turkey that provide a considerable geographic barrier. Reports of insect migration in this region are historically particularly sparse and have tended to focus on the painted lady butterfly (Williams 1930, Morris 1935, John et al. 2001, 2015). However, in the spring of 2018, we observed large numbers of the migratory hoverfly *Eristalis tenax* at the tip of the Karpaz peninsula, north-east Cyprus (Chapman unpubl.). Given the geography of the region and the previous suggestions of migratory routes used by butterflies and insectivorous birds, we hypothesised that Cyprus sits at a strategic insect migration site, linking Africa and the Middle East with Europe. To test this hypothesis, we carried out a systematic study of insect migration in Cyprus during late March–early May of 2019, assessing the migratory assemblage, quantifying migratory traffic rates and arrival bearings, and correlating migration with meteorological conditions and vegetation indices in the wider region in order to assess likely source areas.

Material and methods

Location

The island of Cyprus lies in the east of the Mediterranean Sea, linking the Middle East and North Africa with Europe (Fig. 1A). The north–east of the island tapers to a narrow spit of land known as the Karpaz peninsula, orientated along a NE/SW axis (Fig. 1A, circle); we carried out our observations at the extreme north-eastern tip of the peninsula (coordinates: 35°41'42.8"N 34°35'16.8"E), and all documented insect movement occurred along the SW/NE axis (the great majority south–westwards towards the centre of the island, but occasionally north–eastwards out to sea). The nearest landmasses are Turkey to the north (110 km), Syria to the east (108 km) and Israel to the south (465 km). Our observation site is classed as a special environmentally protection area (SEPA) and consists of rocky calcarenite limestone ground interspersed by small wildflower meadows; the peninsula is approximately 6 m above the sea with sheer cliffs broken by narrow gullies (for more information see Fuller 2010, Özden 2013). All field work took place from 28 March to 5 May 2019.

Insect identification

Identification of migrating butterflies and dragonflies to species level was carried out by eye as they arrived from the sea. Smaller insects such as the Diptera were found to use two gullies in the cliff to reach the tip; the major arrival site was the gully at site 1, while smaller numbers arrived by site 2 (Fig. 1B, labels II and IV). Insects were collected by sweeping a butterfly net across the gully continuously for a total of two minutes, once every two hours between 10:00 and 16:00. Trapped insects were transferred to a mesh cage, counted and identified to at least family level in the field (see the Supporting information for full species list). Some Diptera were collected for further identification by Nigel Wyatt at

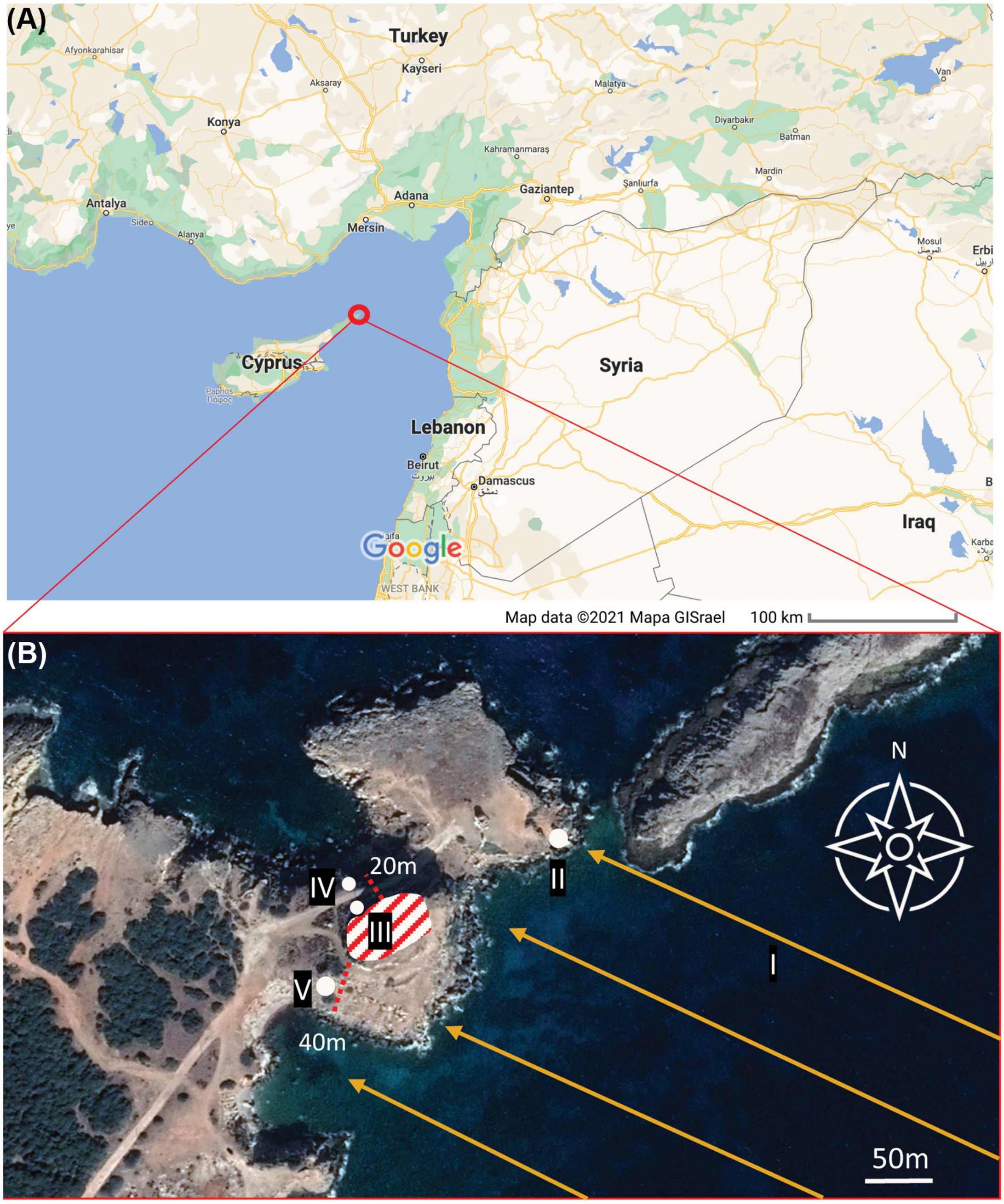

Figure 1. The island of Cyprus and fieldwork location. (A) Cyprus and its position in the Mediterranean. Red circle is location of (B) the tip of the Karpaz peninsula. Numerals indicate: (I) orange arrows: mean direction of insect arrival; (II) location of insect collection (site 1); (III) butterfly/dragonfly counting location; (IV) location of primary camera trap and insect collection point (site 2); (V) location of secondary camera trap. Shaded red/white area: large rock formation above which few small insect migrants were observed. Dashed red lines: widths of insect count observations. Base images taken from Google Earth.

the Natural History Museum, London. It is presumed that the ratio of insects (numbers and classifications) caught and counted is representative of all the insects migrating.

Quantifying the bioflow of larger migrants

We quantified the arrival of migrant butterflies and dragonflies by counting numbers passing through a 15 m wide section of the peninsula (Fig. 1B, label III) during a 15-min period, once every two hours from 10:00 to 16:00. These numbers were then scaled for the remaining two hours between surveys up until 18:00 by multiplying counts by eight to reach two hours. To calculate migratory traffic rate (MTR), we divided the number of insects recorded in a count (N) by the number of minutes recorded (15), before dividing this figure by the width of Karpaz peninsula over which the insect group in question was recorded moving (W). For butterflies this was 15 m (except for the 5 April when the recorded numbers were observed through binoculars with a field of view equal to 8.18 m). For dragonflies, W equals 15 m.

$$\mathrm{MTR} = \left(\frac{N}{15\ \mathrm{min}} \right) / W$$

Two further migratory events required specific approaches. First, on 5 April, an intense painted lady butterfly movement was evident from 06:00 in the morning at our accommodation (Oasis hotel, 35°37'47.0"N 34°22'27.7"E) until 09:30 (location not illustrated in Fig. 1). A 15-min count was performed at 07:35 at the Oasis hotel across a 40 m wide transect by WLSH, and observations 5 km away perpendicular to the migration direction by JWC confirmed that the insects remained migrating at a similar frequency across a 5 km transect across the island. This figure was then multiplied by 14 to estimate total numbers passing between 06:00 and 09:30. Therefore, to calculate the number of butterflies (R1) across the 5 km transect between 06:00 and 09:30 (210 min), we linearly scaled the number counted (N1) per 15 min across the 40-m counted transect.

$$\mathrm{R1} = \mathrm{N1} \times \left(\frac{5000}{40} \right) \times \left(\frac{210}{15} \right)$$

Later the same day at the tip of the peninsula, migration continued but at a considerable height above the ground, estimated to be 60 m. High-altitude counts were obtained using a pair of Swarovski 8 × 30 binoculars with a field of view (FOV) of 7.8°. On this day, the high-flying butterflies were observed to be migrating above all points of the peninsula's width of 230 m and so the entire width of the tip was used to scale the insect's numbers. However, it should be noted that the passage of butterfly migration also continued above the ocean around the tip, making this figure an underestimate of total butterfly numbers. To calculate the number of butterflies (R2) passing across the 230 m wide peninsula tip every two hours (120 min), we again linearly scaled the number counted (N2) per 15 min across the FOV.

$$\mathrm{R2} = \mathrm{N2} \times \left(\frac{230}{60 \times \tan\left(7.8^\circ\right)} \right) \times \left(\frac{120}{15} \right)$$

Second, on the night of 14 April, strong southerly winds bought dust storms from the Sahara and large-scale arrival of rush veneer micro-moths (Crambidae: *Nomophila noctuella*). These insects landed on the tip and were resting during the day. To count them a series of 1 m^2 quadrats ($n = 28$) were used across the 21 069 m^2 tip of the peninsula. The quadrats were placed randomly and the raw counts of moths within them were scaled to encompass the whole area of the tip. However, as these insects arrived overnight, they were not included in the diurnal migratory traffic rate calculations.

Quantifying the bioflow of smaller migrants

Numbers of smaller migrants were quantified from video recordings over a 5 m subsection (Fig. 1, label IV) of a 20 m wide area the insects were migrating through between the sea cliff and the wall of the large rock formation (Fig. 1, shaded area). We utilised a smartphone camera and the Tasker app to automatically record every 30 min for 1 min between 10:00 and 16:00 at 30 fps, 1080 p. On five occasions recordings were taken up until 16:45 when large migratory movements occurred. Recordings were converted to an uncompressed AVI file using FFMPEG software (Tomar 2006) and each frame viewed within ImageJ (Schindelin et al. 2012) to count insects as they passed the halfway point in the field of view. However, due to the recording angle and camera resolution the number of insects detected across this distance attenuated sharply past the 2.5 m mark so the final counts are likely an under-estimate of the true numbers. In addition, only insects larger than a *Melanostoma mellinum* (bodylength: 10 mm) are visible in these recordings, meaning that smaller insects were not reliably registered. As insects larger than 10 mm comprised 23% of our net-caught samples, the remaining 77% of the insects were not detected by the video trap. To account for this, an estimation of the missed insect numbers has been provided in the results alongside the raw counts.

Scaling raw insect counts

We scaled these raw insect counts to get a more representative estimation of the insects migrating onto the tip of the peninsula (Equation: R3). To scale for time, raw counts (N3) were multiplied by 30 to obtain representative counts for 30 min. To scale for the width of this migratory pathway (of 20 m), the raw counts (N3) made over a 5 m width were multiplied by 4.

$$\mathrm{R3} = \left(\mathrm{N3} \times \left(\frac{30}{1} \right) \times 4 \right)$$

Insect counts at location 2

On 2 May (the largest 'mass migration' day) raw counts (N4) between 14:30 and 16:00 (the peak of insect movement) from a secondary location (between the southern edge of the large rock formation and the ocean; Fig. 1, label V) were performed simultaneously to counts at location 1. The counts were recorded across 2 m before being scaled up to the entire 40 m width. It was noted that the insects were migrating over an area extending into the sea and making landfall further to the SW, suggesting that the counts are an under-estimation of the true numbers. On other 'mass migration' days insects were also observed to be migrating around the south of the large rock formation, regrettably on these days regular video trap counts were not taken from location 2. Total insect numbers from site 2 (R4) were calculated using the following equation:

$$\mathrm{R4} = \left(\mathrm{N4} \times \left(\frac{30}{1}\right) \times 20\right)$$

Insect headings and migratory traffic rate (MTR) calculations

Movement directions of smaller and larger insects onto mainland Cyprus were also recorded. Individuals moving NE were not classified as migrating (with one exception) as they were not observed leaving Cyprus towards the east over the sea and appeared to be undertaking local foraging movements. To avoid double counting of the randomly foraging insects, we assumed an equal amount to those moving NE would be represented in our SW migrant counts and subtracted this number from these counts before analysis of the migratory population occurred. To calculate migratory traffic rate (MTR), we divided the number of insects recorded per minute (N) by the width over which the recording was made (W). For the video trap at location 1 this width was 5 m. For when location 2 was used on 2 May, the width was 2 m.

$$\mathrm{MTR} = \frac{N}{W}$$

Meteorological data

Weather conditions were recorded every 2 h between 10:00 and 16:00 each day. Measurements included cloud cover recorded in the Okta scale (UKMO 2010), windspeed and wind direction in m s^{-1} using a Windmate Anemometre, temperature in degree Celsius using the Windmate's built in thermometer and precipitation as dry or raining.

Exploring geographic origins with NDVI data

The normalised difference vegetation index (NDVI) measures the difference between red light (which vegetation absorbs) and near-infrared (which vegetation reflects strongly) to quantify vegetation. NDVI data was collected from the NASA provided GIMMS Global Agricultural Monitoring (GLAM) interface. We searched MODIS (moderate resolution imaging spectroradiometer) NDVI imagery and collected time series data from the TERRA MODIS 8-day NDVI anomaly dataset over the years from 2000 to present from the regions immediately surrounding Cyprus that represented putative natal origin areas. A positive anomaly reading would indicate that more vegetation was present at the time of the reading when compared to the area mean.

Calculating the total numbers of insect migrants leaving the Middle East

We used the following steps and assumptions to scale from the catch data to the number of insect migrants leaving the Middle Eastern mainland:

1) Hoverflies and other insects can resolve and target objects that subtend visual angles (V) as small as 0.2° (Nordström et al. 2006, O'Carroll and Wiederman 2014).
2) The Karpaz peninsula when approached from the east is $a = 100$ m wide and $b = 6$ m high.
3) Based on the height of the peninsula, the hoverflies and other insects would be able to resolve the land as a small object at a limiting distance (D) where:

$$D = \frac{b}{V}$$

(V is measured in radians).

4) From this calculation, we determined that under perfect conditions, insects could see Cyprus from a maximum of 1719 m away.
5) All the insects able to see the peninsula were assumed to cross over land as it allows a the opportunity for landing (Wikelski 2006).
6) The proportion of the migration front that all the insects counted on the peninsula came from was modelled as the circumference of the arc at resolvable distance of the island.
7) We then estimated the total number for migratory insects (Supporting information) as the overall length of the migration from the Middle East, divided by the arc length multiplied by the number of insects counted in Cyprus.

Nutrient transfer calculations

We estimated the amount of nitrogen and phosphorus contained in the insects' bodies from insect weights obtained from various publications (Supporting information). Where only dry weights were available, the true fresh weight of each insect was estimated as in Mellanby (1958) assuming insects consist of ~75% water. Individual insect weights were then multiplied by the number of individuals travelling to Cyprus. To estimate the total weight of all the insects moving from the Middle East into western Europe, individual insect weights were also multiplied by the scaled figures for the total number of insects migrating. Insect bodies are known to consist of ~10% nitrogen and 1% phosphorous (Finke 2002) and we used these figures to calculate the total mass of these nutrients transferred by the migrants.

Statistical analyses

To identify the days constituting the majority of migration activity, we divided days into 'mass migration days' and 'non-mass migration days'. In brief, we ordered all the days in the season by number of insects recorded from highest to lowest and selected all migration occasions as 'mass migration' events until they cumulatively reached 95% of the total number of individual insects recorded in the season. Wind directions and arrival bearings were analysed using a Rayleigh test of uniformity to give a mean direction, resultant length (r-value) and an associated p-value. t-tests and linear regressions were used to compare windspeed and temperature to migration traffic rate and to determine if NDVI anomaly scores for 2019 from countries in the Middle East region were significantly different to the mean (2001–2018) values from that country. All figures and statistical analyses were produced using R ver. 4.0.2 and the circular package (Agostinelli and Lund 2017, <www.r-project.org>).

Results

Assemblage of insects migrating onto Cyprus

The complete migratory assemblage of diurnal insect migrants (but also including the only major nocturnal arrival that was witnessed, comprising of 900 000 *Nomophila noctuella* moths which were observed grounded in the day) consisted of eight insect orders, in the following proportions: flies (Diptera, 86%), butterflies and moths (Lepidoptera, 10%), bees and parasitic wasps (Hymenoptera, 2%), true bugs (Hemiptera, 1%), dragonflies (Odonata, 0.5%), beetles (Coleoptera, 0.3%), bark lice (Psocoptera, 0.06%) and lacewings (Neuroptera, 0.01%) (Fig. 2A, Supporting information). Within this assemblage, 30 insect families were represented, with the three most abundant all being Diptera: Anthomyiidae (39%), Syrphidae (17%) and Sepsidae (10%) (Fig. 2B). The most abundant species by far was the bean seed fly *Delia platura* which made up 99% of the Anthomyiidae. Identification of the ecological roles of this assemblage from the literature found the most numerous were pollinators (98%), followed by pests (48%), decomposers (16%) and pest predators (4.4%) with all contributing to nutrient transfer (Supporting information).

Quantifying migratory bioflows onto Cyprus

In total, scaled counts reveal just under three million (2 981 526) butterflies migrating onto the tip of the Karpaz peninsula, Cyprus. More than 99% of these were painted ladies *Vanessa cardui* with 99.8% (2.98 million) of the whole season's butterfly counts seen on 5 April (Fig. 3A, B). Of the total number 99.5% were moving west as opposed to east. Total counts for dragonflies were 304 409 of which over 99% were vagrant emperors (*Anax ephippiger*) with 185 000 arriving between 1 and 4 April (Fig. 3A, B). In contrast to the other migrants whose populations moved overwhelmingly to the west, on 8 April 110 000 vagrant emperor dragonflies were seen actively leaving Cyprus across the sea to the NE. Both the Lepidoptera and dragonflies only appeared in large numbers at the beginning of April and not again during the rest of the field season.

In total, linearly scaled counts put the net flow of moving insects detected by the video trap (sites 1 and 2) at just over 8.4 million. When the insects that are too small to be detected by the video trap are also added, this figure rises to 36.4 million. While the larger butterflies and dragonflies were found to be most abundant during the early field season (1–5 April), smaller insects were most abundant at two distinct timings: early season (28 March–5 April) and late season (25 April–4 May) during which time numbers peaked at over 11 million insects (Fig. 3A, B). The grand linearly scaled total for all diurnal migrants arriving on Cyprus via the Karpaz peninsula is 39.6 million insects, with migration traffic rates (MTR) varying from 1 to a peak recording of 1779 insects $m^{-1}min^{-1}$ at location 1 (Fig. 1B, label IV), and 1 to > 5900 insects m^{-1} min^{-1} at location 2 (Fig. 1B, label V) (Supporting information).

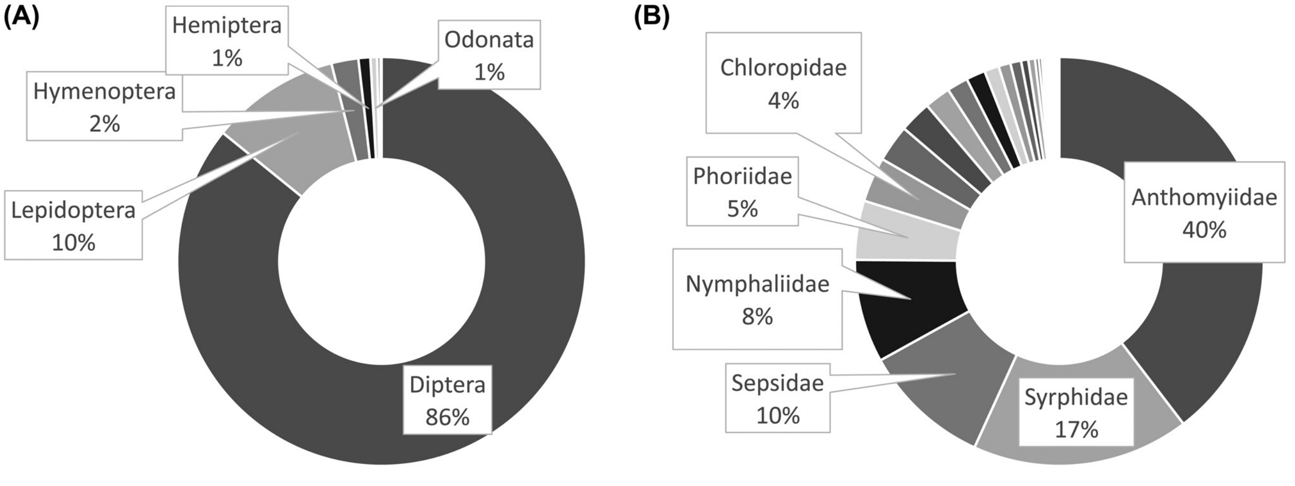

Figure 2. Cyprus migratory assemblage. (A) Proportion of migratory assemblage by order. (B) Proportion of migratory assemblage by family. See the Supporting information for a full species list.

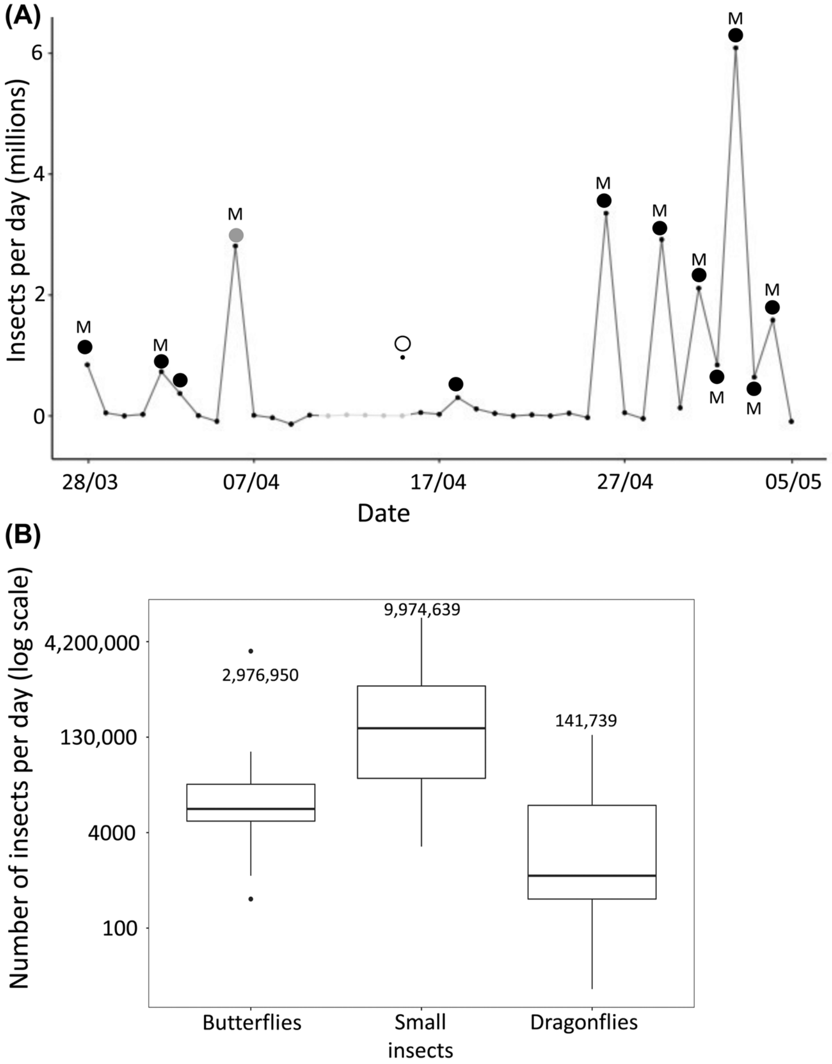

Figure 3. (A) Total number of insects per day recorded at location 1 (Fig. 1B, label IV). Shades indicate main insect type on each peak: black indicates Diptera, grey is butterflies, the white circle with an unconnected dot below represents the nocturnal arrival of *Nomophila noctuella* moths (this is not included in the migration rate). An M above the peak indicates a mass migration day. Greyed-out data points between 10 April and 15 April indicate a lack of video trap data due to camera being stolen, Lepidoptera/dragonfly counts still present. For migratory traffic rate (MTR) values see Supporting information. (B) Number of insects per day of the main insect groups (butterflies, small insects and dragonflies) plotted on a log scale. Location 1 and 2 (Fig. 1B, label IV and V) were included for the small insect calculations. Solid black bars represent the medians, boxes represent the inter-quartile range (IQR), whiskers extend to 1.5× the IQR, dots represent outliers. Numbers above the bars represent the largest totals recorded on a single day for each group.

Nocturnal migrants

Although nocturnal insect migration was not systematically monitored, on the night of 14 April 905 967 rush veneer moths (*N. noctuella*) arrived. This event coincided with a large dust storm and southerly winds on 13 April suggests that the origin of these moths could have originated in the Sahara or the Rub' al Khali desert of Saudi Arabia.

Influence of weather on migratory events

To investigate the influence of temperature, wind direction and wind speed we analysed the relationship of these factors with 'mass migration' versus 'non-mass migration' events. In total, 10 days were classed as mass migration events and 25 as non-mass migration events (Fig. 3A). In general, mass migration events occurred with a mean downwind direction towards the west (Fig. 4A, black arrow and dots; Rayleigh test: 274.5°, $r = 0.61$, $p = 0.02$), while the largest migration days also coincided with a westward downwind direction (Fig. 4A, dotted lines). In contrast, on non-mass migration days, wind directions were random (Rayleigh test: $r = 0.08$, $p = 0.84$) with peak migration rates 34 times smaller than on mass migration days (Fig. 4B). Mass migration days were also associated with warmer temperatures ($t = -2.5$, $p = 0.01$), averaging 21.5°C in contrast to 19.3°C on non-mass migration days (Fig. 4C),

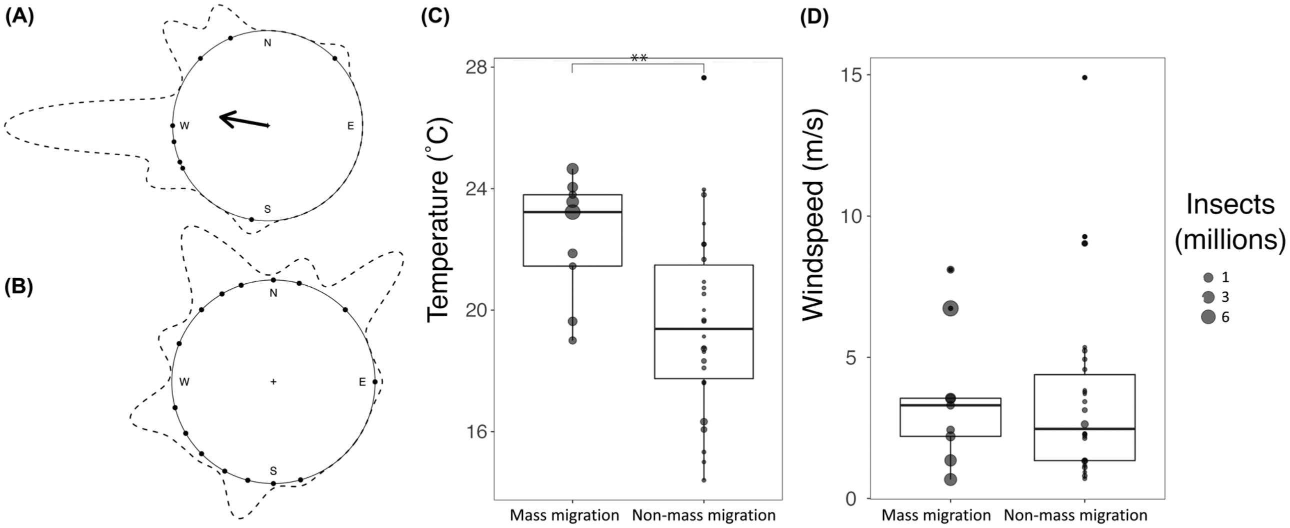

Figure 4. Influence of wind direction, temperature and wind speed on migration. (A, B) Circular plots showing downwind direction (black dots), wind mean direction (black arrow) and the circular density of insect numbers (dotted line) on mass migration (A) and migration (B) days. Note that density plots are not to scale, the largest peak in A is 18.8 times larger than the largest day in B. (C, D) Relationship between temperature (C) and windspeed (D) with mass migration and migration days. Migration rates are expressed as insects day^{-1}.

while windspeed did not significantly affect migration rate ($t = -0.05$, $p = 0.96$; Fig. 4D).

Exploring geographic origins with NDVI data

Vegetation growth detected by high normalised difference vegetation index (NDVI) values have been associated with insect emergence, especially in arid/semi-arid regions (Renier et al. 2015, Hu et al. 2021). We identified six countries surrounding Cyprus where spring 2019 NDVI values were significantly higher than the long-term mean (2001–2018) (Supporting information). Syria showed the largest NDVI anomaly score followed by Iraq, Lebanon, Iran, Saudi Arabia and Jordan (Fig. 5A and B). Other countries immediately surrounding Cyprus (Turkey, Egypt, Israel and the region of Palestine) did not show significant increases in NDVI values. Areas of highest NDVI anomaly values were identified in Syria in the lowlands around Lake Asad and the Euphrates River as well as the Jabal Abu Rujmayn mountain ranges (Fig. 5A). In Iraq, the highest NDVI anomaly values were found in the desert regions to the south (near Al-Muthannā) as well as just south of the Mesopotamian marshes, and desert regions to the west of the country (the Al Anbār region). In Saudi Arabia, the highest NDVI anomaly values were focused on the region around Medina and northeast near Sakaka. Further afield, western Iran and specifically the Kuh Giluya region also showed high NDVI anomaly values.

Total number of insects leaving the Middle-East

As wind and NDVI data suggest that insects arrived in Cyprus from the east, we estimated the total numbers of insects leaving this region. Our calculations based on a visual 'funnel of attraction', and under a scenario of local insect emergence, suggest 115 million insects would have left a 10 km region adjacent to Cyprus. This increases to 1.15 billion with a 100 km front, 3.45 billion with a 300 km front and 6.9 billion with a 600 km front encompassing the entire Mediterranean coastline of the Middle East (Supporting information).

Discussion

In this study we document a hitherto underappreciated major migration route of insects from the Middle East region into southeast Europe and identify a suite of new insect migrants. We estimate that during our observation period (39 days from 28 March to 5 May 2019), over 39 million insect migrants arrived in Cyprus via the extreme tip of the Karpaz peninsula in the northeast of the island, after a sea crossing from the Middle East region more than 100 km to the east. These insects arrived in intense peaks of activity, the maximum being over 5900 insects m^{-1} min^{-1}. The migratory assemblage was highly diverse, being composed of 30 families from eight orders. To the best of our knowledge, this is the first time that the complete diurnal insect migrant assemblage has been documented, and the scale of the migration quantified, in this region. The 39 million insects arriving in a very small region of Cyprus (the point of a peninsula just a few 10s of metres across) were clearly just a very small proportion of the total flow of insects across the eastern Mediterranean Sea from the Middle East, the great majority of which would have either died in the sea before reaching Cyprus, made landfall somewhere else along the eastern coastline of Cyprus or missed Cyprus altogether and passed further westward to the south and/or north of the island. The challenges of recording such movements over a larger area, and limitations in methodology, have likely led to significant underestimates of the true numbers of migrants making landfall. Moreover, because we

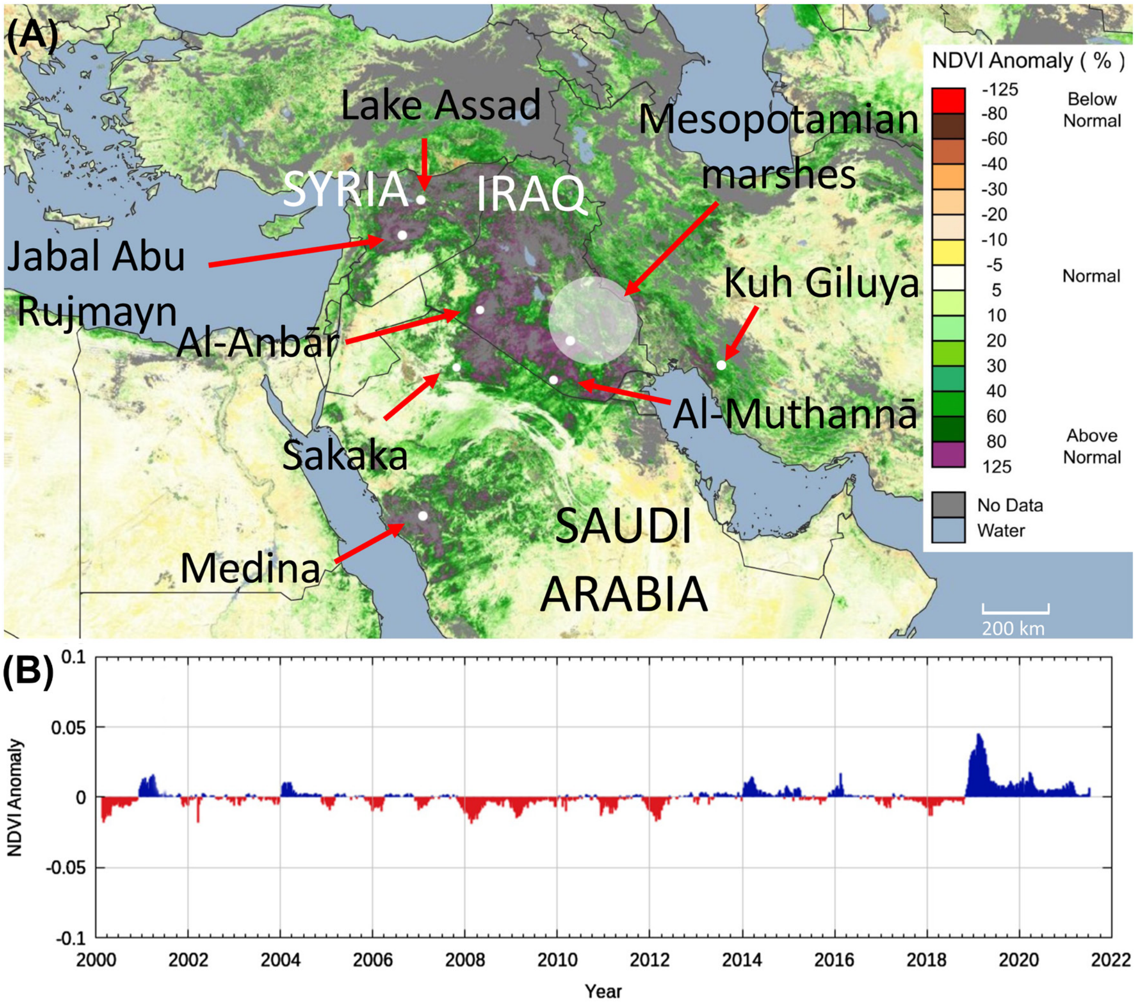

Figure 5. NDVI mapping of the countries surrounding Cyprus. (A) map showing the NDVI anomaly scores for the Middle Eastern region of spring 2019. Areas of Syria, Iraq and Saudi Arabia show highest NDVI anomaly score (purple and dark green; see legend). (B) NDVI anomaly values between 2000 and 2021 for the combined areas of Syria, Iraq and Saudi Arabia.

sampled only the flight boundary layer (FBL) of insect migration, there could have been far more insects migrating high overhead as has been shown in studies using entomological radars (Hu et al. 2016, Wotton et al. 2019) and high-altitude sampling (Chapman et al. 2004). Although we have no way of confirming this, we believe that because the insects have just flown at least 100 km across open water to reach Cyprus, the majority will have become sensitive to cues from land which would tend to initiate decent and alighting. To confirm whether insects are indeed migrating at high altitude above the field site, further investigations utilising an entomological radar are needed. In addition, while it is not possible for us to accurately predict the scale of the migration, we have made some estimates based on different lengths of potential migratory fronts leaving the Middle Eastern coast; these indicate that the total bioflow of insects departing the coastline of Syria and/or Israel was probably in the hundreds of millions, and perhaps in the billions of individuals.

While systematic observations of nocturnal migrations were not performed, with the exception of a large-scale arrival of *Nomophila noctuella* moths on the night of 14 April, we expect that there were considerable numbers of nocturnal insect migrants flying across the region in spring 2019. Future studies, into the nocturnal migrants would be of great interest and are likely to uncover an assemblage dominated by the Lepidoptera, while species groups such as the Staphylinidae rove beetles and the Homoptera may also be abundant, as was the case during a nocturnal insect migration survey across Mali (Florio et al. 2020).

Diptera (the true flies) were the most abundant group of migrants, making up 86% of all individuals recorded (Fig. 2A). Diptera are often highly abundant within studies of migratory assemblages, but rarely the most numerous order (Hardy and Milne 1938, Freeman 1945, Chapman et al. 2004) and this is especially so above agricultural areas where aphids (Hemiptera) typically dominate. The hoverflies (Syrphidae), comprised 17% of all migratory insects recorded and are some of the best studied dipteran migrants (Wotton et al. 2019, Doyle et al. 2020, Gao et al. 2020), however, one species of Anthomyiidae dominated the fly assemblage, *Delia platura* (Anthomyiidae) which made up 46% of the Diptera and 39% of the total migrants detected entering the Karpaz peninsula (15.4 million individuals). We found a single previous report of migratory behaviour in this species (Kurahashi 1991) which is a generalist crop pest affecting nearly 50 different plant species (Guerra et al. 2017). These include economically important crops such as soybeans, corn, beans, peas, onion, potato, tobacco, strawberry, wheat and garlic (Kessing and Mau 1991, Erdogan 2020). In addition, this species has recently been discovered as a major vector of the soft rot bacteria (Pasanen 2020), a finding made more important with the documentation of the migratory potential of *D. platura*. It has a global distribution (it is found on all continents except for Antarctica (Griffiths 1993)) and its abundance in crops in areas such as the UK is thought to be increasing (Ellis and Scatcherd 2007). The migratory potential of *D. platura* could have serious consequences for pest management strategies, because as is the case in the diamondback moth *Plutella xylostella*, migratory behaviour can facilitate the spread of insecticide resistance within the population, and it is expected that resistance found in other migratory crop pests may spread in a similar manner between populations (Wang et al. 2021). However, this species also has important pollination potential, and its positive influence is detailed below.

Butterflies made up 10% of all individuals recorded. The vast majority (> 99%) of the butterfly species recorded during the field season on Cyprus were the painted lady *Vanessa cardui*. This is somewhat surprising given the range of other potential migrant butterflies found around the Middle East, such as *Croceus crocea* (clouded yellows) and the red admiral *Vanessa atalanta* (Chowdhury et al. 2021) and suggests that painted lady butterflies may be better able to maximise the potential of desert vegetation bloom after rainfall, as discussed below. The migrations in the spring of 2019 in Cyprus appear to have been exceptional in terms of numbers (Benyamini 2019, Shalmon and Benyamini 2019) but not without historical precedent. Previous observations from this area have focused on the painted lady butterfly (Morris 1935) with the most recent large-scale movement across Cyprus recorded in 2001 where an estimated 48 million crossed a 200 km front of Cyprus from north to south (John 2001). During the 2001 migration event, painted lady butterflies were supposed to have migrated through the night to reach Cyprus (John 2001). While we recorded large numbers of butterflies migrating further inland during the early morning of 5 May, we believe that these individuals roosted on Cyprus the night before. We do not dispute the claim that painted lady butterflies can migrate nocturnally, but we did not see any evidence of this during our field-season and expect that they only perform this behaviour out of necessity. Migration traffic rates of butterflies in Israel during Spring 2019 reached a peak of 90 individuals m^{-1} min^{-1} recorded at Mount Gilboa on 21 March (Benyamini 2019), 10 times the peak counts during our field season in Cyprus (9 m^{-1} min^{-1}).

Dragonflies, specifically the vagrant emperor *Anax ephippiger*, made up 0.5% of all individuals recorded. Like the butterflies, the dragonfly assemblage was dominated by a single species, the vagrant emperor with just under 195 000 individuals estimated to have arrived onto the tip of the Karpaz peninsula. The arrival of 140 000 on 1 April represents the largest known migration event of this species onto the island, with the last recorded large-scale arrival occurring in 2004 and numbering in the 'many thousands' (Flint 2019). Unlike all other migrant insects, vagrant emperors were also observed leaving the island heading northeast. It is unclear why this difference should exist, but we noted predatory behaviour and movement in relatively discreet groups during migration that warrant further investigation into the sociality of insect migration. There is also the possibility it was the same group of migratory dragonflies that arrived from the east that headed back north-east again a few days later. This dragonfly was also recorded breeding for the first time in the Netherlands in 2019, providing more evidence that the migration in 2019 was especially notable (Manger 2020).

Of all the migrants recorded, the majority reached the island on 10 mass migration days during which the downwind direction was favourable for the insects moving west and the temperature was warmer. Insects are known to utilise favourable winds to aid their migration (Wikelski et al. 2006, Chapman et al. 2008, Gao et al. 2020, Knoblauch et al. 2021) and we found that on days where mass migration occurred, the average wind direction was towards the west. While north may well be the preferred direction of at least the larger species during the spring migration season (Gao et al. 2020), downwind transport is often used to conserve energy and maximise distances travelled (Chapman et al. 2011, 2016). In support of this we note reports of headings varying through west to northeast over Israel but only few observations of southward headings (Benyamini 2019) suggesting that the insects are 'going with the flow' when wind directions can assist movement in roughly the right direction. For example, this behaviour has been documented in hoverflies arriving in spring in the UK, that show weaker orientation tendencies compared to autumn migrants, and do not correct for wind drift away from their seasonally adaptive direction (Gao et al. 2020). We found no clear effect of windspeed on migration, but mass migration events were significantly associated with warmer temperatures, as has previously been found in migrations of monarch butterflies *Danaus plexippus* and dragonflies *Aeshna mixta* and *Sympetrum vulgatum* (Knight et al. 2019, Knoblauch et al. 2021). Therefore, warmer temperatures and winds from the east serve as useful predictors for mass migration events for spring migrations across Cyprus and could be integrated into predictive models for insect movements in this region.

Our work has revealed a major migratory flyway of insects from the Middle East into Europe during the spring. Although more research over multiple years is required to confirm this, it is possible that this great Eastern Flyway is a regular springtime route for migratory insects repopulating Europe. Analysis of NDVI datasets showed that the areas with comparatively high values during winter 2018 and spring 2019 were parts of Syria, Iraq, Saudi Arabia and Iran up to 1600 km distant from Cyprus. This large area suggests a broad front of migration leaving the east, that at its maximum, may be equal to the Mediterranean coastline of the Middle East, approximately 600 km in length. This calculation leads to the maximum estimation of 6.9 billion insects leaving the Middle East and heading west. This number includes 5.9 billion flies, 2.7 billion *Delia platura* Anthomyiid flies, 1.17 billion hoverflies, 690 million painted ladies and 35 million dragonflies. The size of the spring migration of 2019 was likely to have been exceptional given the higher-than-average NDVI scores, and it remains to be seen how much migration occurs in more typical years. One area with the highest NDVI increases above the 20-year mean was just south of the Mesopotamian marshes of Iraq. These wetlands may have provided the perfect habitat for many of the larval stages of dragonflies and the aquatic larvae of the hoverfly *Eristalis tenax* (van Veen 2010, Dijkstra and Schröter 2020). However, this area has undergone large-scale agricultural expansion within the last 50 years, changing much of the natural marshland into fields for crop growth (Al-Quraishi and Kaplan 2021) and this may have shifted the historical balance towards the vast numbers of *D. platura* crop-pest flies recorded.

In contrast to the flies and dragonflies, painted lady butterflies may have originated primarily in the deserts of western Saudi Arabia. Painted lady caterpillars are known to develop on rapidly growing plants that respond quickly to water availability in arid regions (Ackery 1988, Benyamini 2017, Hu et al. 2021). Water availability for plant growth in winter is closely linked to a high NDVI value and is associated with larger populations of herbivorous insects (Schlaich et al. 2016). Millions of painted ladies emerged in the Negev desert of Israel during winter 2015/2016 following abnormally high rainfall in the area that led to increased growth of the forbs *Forsskaolea tenacissima* (Urticaceae) and *Malva parviflora* (Malvaceae) (Benyamini 2017). NDVI scores in winter 2018/2019 indicted that large areas of previously highly-arid deserts in northern and western Saudi Arabia experienced atypically high rainfall and plant growth, conditions likely facilitating mass painted lady emergence during spring 2019. A large proportion of the painted lady butterflies observed in Israel during the study period were noted to be migrating northeast, as well as northwest (Benyamini 2019). This suggests that the movement of migratory insects during spring 2019 was not limited to those headed west like those recorded on Cyprus, but was far bigger with migratory directions potentially covering other compass headings.

Ecological roles of the migratory assemblage

Migrants are uniquely placed in global ecosystems as 1) 'genetic links', transporting substances such as pollen; 2) 'resource links', transporting organic matter such as nitrogen and phosphorous within their bodies; and 3) 'process links', through trophic interactions that structure food webs and therefore biodiversity patterns (Lundberg and Moberg 2003, Jeltsch et al. 2013, Satterfield et al. 2020). These roles are well known from migratory vertebrates but have been mostly overlooked in migratory insects. Of the insects migrating into Cyprus, we found the most numerous roles played were as pollinators (98%), followed by pests (43%), decomposers (16%) and pest predators (4.4%) with all contributing to nutrient transfer.

Of all migratory insects 98% were pollinators: these include the Syrphidae (17%), shown to visit over 50% of major global food crops (Doyle et al. 2020); the Anthomyiid *D. platura* (39%), known to be a highly effective *Brassica* crop pollinator (Stavert et al. 2018); and the painted lady butterflies (8%). In total, a potential maximum of 6.52 billion pollinators are estimated to have left the Mediterranean coast of the Middle East travelling towards the west during Spring 2019. We observed *E. tenax* hoverflies and *Calliphora* blowflies making landfall after a > 100 km sea crossing with orchid pollinia attached to their heads (Fig. 6A, B), indicating the capacity for long-distance pollen transfer, and hinting at the potential of these movements to enable cross-continental gene flow on a massive scale. Future investigations into this could explore how migratory pollinators might aid in the adaptions for plant populations to a warming climate by spreading favourable alleles for drought or disease resistance (Luo et al. 2019) or to support the health of isolated plant populations (Pérez-Bañón et al. 2003).

In addition, like many pollinators, migratory pollinators are under threat (Gatter et al. 2020) and landscape connectivity may be particularly crucial, underlying the strategic position of Cyprus and the importance of its floral resources for this phenomenon (Nabhan 2004, Doyle et al. 2020). The importance of connectivity of landscape – for example in the provision of sequentially blooming floral resources – continues across the whole migratory pathway and the lack of this connectivity is likely a major driver of some migratory insect declines. Wildflower meadows are being lost across Europe due to climate change, intensified agriculture and other anthropogenic land use (Goulson et al. 2005, Warren et al. 2021) and protection of the phenomena of large-scale insect migration, should consider how to conserve key areas along migration corridors (Rischen et al. 2021, Thomas et al. 2021).

Many of the dipteran migrants identified here also play important roles in decomposition, with around 16% involved in this process. These include the Sepsidae whose larvae tend to feed on decaying animal corpses (Oleksakova et al. 2016) and hoverflies in the subfamily Eristalinae that numbered just under 6% of all insects migrating. Eristaline hoverflies contribute to the breakdown of organic matter in many natural habitats as well as contributing to the breakdown of slurry from livestock. As such, these populations contribute to reducing the impacts of farming, climate change, eutrophication and acidification (Yuan and Pollard 2018).

All the insects leaving the Middle Eastern Mediterranean coast and heading west contributed to nutrient transfer, and following death, their nutrients return to the soil or are taken up by other organisms (Chapman et al. 2015). Migrant insects contain nutrients that are limiting to plant

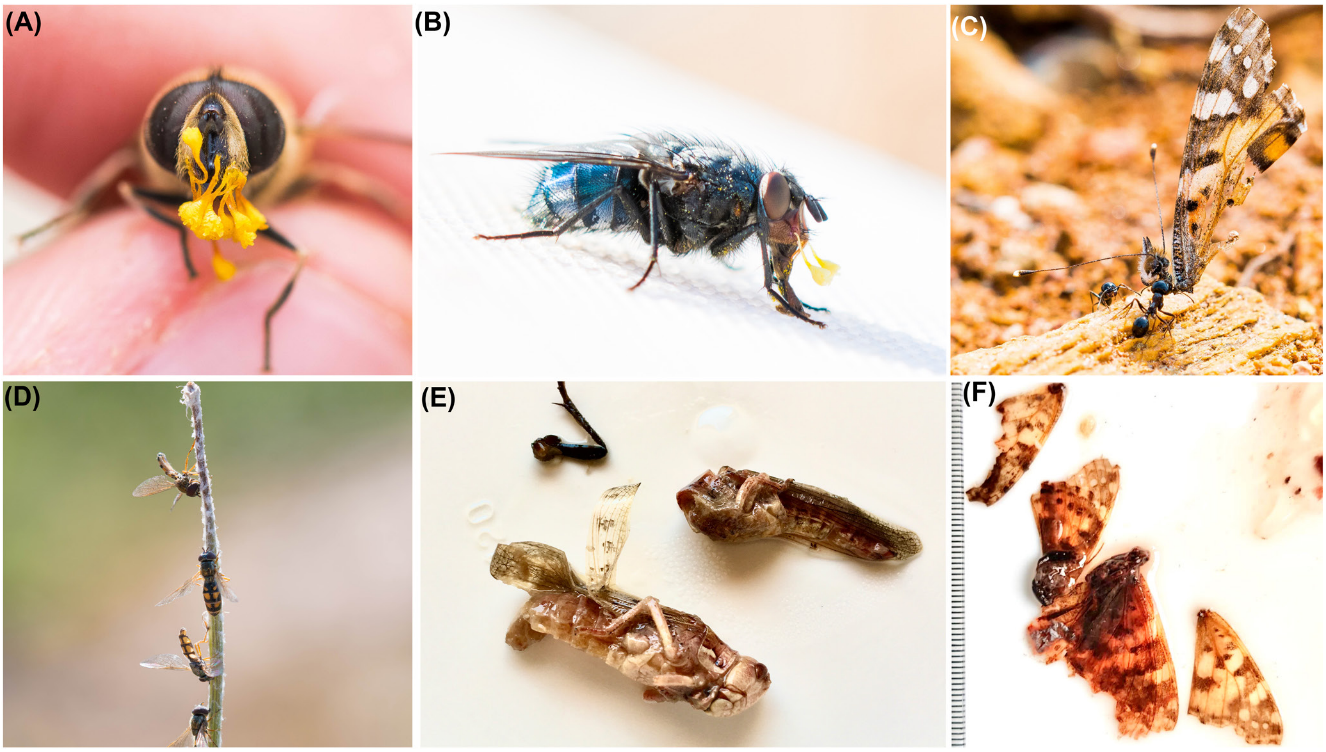

Figure 6. Examples of insects carrying out ecological roles in Cyprus during the 2019 Spring migration field season. (A, B) An *Eristalis tenax* hoverfly and *Calliphora* sp. blowflies caught making landfall after a > 100 km sea crossing with orchid pollinia on their heads, indicating their capacity for cross-continental pollen transfer. (C) *Formica* ant species consuming a migratory painted lady. (D) *Melanostoma mellinum* hoverflies infected by a fungal pathogen. (E, F) Migrants as a food source in the ocean: (E) Orthopteran removed from green turtle stomach (©Olivia Forster) and (F) painted lady butterflies *Vanessa cardui* removed from loggerhead turtle stomach (©Josie Palmer).

activity, namely nitrogen (N) and phosphorous (P) (Landry and Parrott 2016). The maximum total of all the migrant insects leaving the Middle East amounts to 275 tonnes of biomass, made up of 27.5 tonnes N and 2.75 tonnes P (Elser et al. 2000) for chemical make-up of insects). Though not the most numerous, the largest contribution to this biomass came from the painted lady butterfly (141 tonnes). These various insect migrants may also be important as a huge influx into local food webs, both terrestrial and aquatic (Fig. 6C, E, F) as well as displaying functional links between the co-migrants (predator–prey, host–parasite interactions etc.) and pathogens (Fig. 6D) (Cohen and Satterfield 2020). For example, we observed painted lady butterflies being eaten by ants (Fig. 6C), hoverfly mortality caused by entomopathogenic fungi (Fig. 6D), vagrant emperor dragonflies being taken by falcons (while they too were migrating), hoverflies and other Dipterans being taken by birds such as swifts and wood-warblers, and both migratory Orthoptera and painted ladies were found within the stomachs of dissected loggerhead and green turtles found stranded on a Cyprus beach in spring 2019 (Fig. 6E, F; Forster unpubl.; Palmer 2021). These observations highlight the extent of nutrient transfer and food web structuring by migratory insects and hint at the importance of these transient events for linking geographically separated ecosystems.

Conclusion

We identified Cyprus as an important migratory hotspot for springtime insect movement and documented the species assemblage and numbers using an Eastern Mediterranean Flyway as a route into Europe from the Middle East. The Middle Eastern region is likely to form an important developmental ground for insects spending their summers in Europe. The large numbers of insects recorded, and the wide array of ecosystem functions that they perform across continents, marks this movement as an important process by which insects interact with each other and with the environment through which they transit. We have detailed the roles these insects play, including new observations of migratory behaviour in the emerging pest species *Delia platura* (Ellis and Scatcherd 2007), and for cross-continental pollen and nutrient transfer. These processes are likely to have important consequences for humans involved in agriculture across the region and at destination locations in Europe. Given the potential ecological impacts of this movement of insects, more research is undoubtedly needed into the phenomenon of insect migration in this area.

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Author contributions

Will L. S. Hawkes: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Edward Walliker**: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (supporting). **Boya Gao**: Investigation (equal); Methodology (equal). **Olivia Forster**: Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Katharine Lacey**: Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Toby Doyle**: Data curation (equal); Writing – review and editing (supporting). **Richard Massy**: Validation (equal); Writing – review and editing (equal). **Nicholas W. Roberts**: Formal analysis (supporting); Methodology (supporting); Validation (equal); Writing – review and editing (equal). **Don R. Reynolds**: Writing – review and editing (equal). **Özge Özden**: Methodology (supporting); Project administration (equal). **Jason W. Chapman**: Funding acquisition (equal); Methodology (supporting); Project administration (equal); Supervision (equal); Writing – review and editing (equal). **Karl R. Wotton**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Supervision (lead); Validation (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.20410992.v1> (Hawkes et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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