

1 **Prediction of migratory routes of the invasive fall armyworm in eastern China**
2 **using a trajectory analytical approach**

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20 **Abstract**

21 **BACKGROUND:** The fall armyworm (FAW), an invasive pest from the Americas, is rapidly
22 spreading through the Old World, and has recently invaded the Indochinese Peninsula
23 and southern China. In the Americas, FAW migrates from winter-breeding areas in the
24 south into summer-breeding areas throughout North America where it is a major pest of
25 corn. Asian populations are also likely to evolve migrations into the corn-producing regions
26 of eastern China, where they will pose a serious threat to food security.

27

28 **RESULTS:** To evaluate the invasion risk in eastern China, the rate of expansion and future
29 migratory range was modelled by a trajectory simulation approach, combined with flight
30 behaviour and meteorological data. Our results predict that FAW will migrate from its new
31 year-round breeding regions into the two main corn-producing regions of eastern China
32 (the North China and Northeast China Plains), via two pathways. The western pathway
33 originates in Myanmar and Yunnan, and FAW will take four migration steps to reach the
34 North China Plain by July. Migration along the eastern pathway from Indochina and
35 southern China progresses faster, with FAW reaching the North China Plain in three steps
36 by June and reaching the Northeast China Plain in July.

37

38 **CONCLUSION:** Our results indicate that there is a high risk that FAW will invade the major
39 corn-producing areas of eastern China via two migration pathways, and cause significant
40 impacts to agricultural productivity. Information on migration pathways and timings can be
41 used to inform integrated pest management strategies for this emerging pest.

42 **Keywords:** *Spodoptera frugiperda*, Asian migration arena, East Asian monsoon, invasive

43 species

44 1 INTRODUCTION

45 The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is a pest noctuid moth that
46 principally attacks corn (maize) but has a wide host range. It is native to the New World,
47 where it breeds continuously in tropical and sub-tropical regions of the Americas, but also
48 has migratory populations that invade temperate North America every spring.^{1, 2} In
49 January 2016 an outbreak of FAW was discovered in West Africa (Nigeria and Ghana),
50 and since this initial outbreak it has spread throughout the Old World at a phenomenal rate.
51 Within two years of arriving in West Africa it had reached almost all countries in
52 sub-Saharan Africa.³⁻⁵ In May 2018, FAW were discovered in Karnataka in southwest India,
53 and by late-2018 FAW outbreaks had been found considerably further east, in Myanmar
54 and northern Thailand.⁶⁻⁸ Its presence in China was confirmed when larvae found in corn
55 in southwest Yunnan province (southwest China) were identified in January 2019 as
56 FAW.^{9, 10} By April 2019 it had spread through much of Yunnan, and also reached the
57 southern Chinese provinces of Guangxi, Guangdong, Guizhou and Hunan (see Fig. 1), as
58 well as Laos and Vietnam.^{11, 12}

59 FAW can survive over-winter throughout most of Southeast Asia (Myanmar, Thailand,
60 Laos, Cambodia and Vietnam) and also in the sub-tropical provinces of China (Yunnan,
61 Guangxi, Guangdong, Hainan, Fujian and Taiwan) lying approximately south of the Tropic
62 of Cancer.¹³ It is highly likely that FAW populations breeding year-round in these regions
63 will evolve annual spring migrations northwards into eastern China (and presumably south
64 again the following autumn), just as FAW populations in North America migrate annually
65 between the northernmost winter-breeding areas (south Texas and south Florida) and the

66 northern United States.^{1,2}

67 The caterpillars of FAW have a very wide host range, and are known to damage more
68 than 180 species of plants.¹⁴ Corn is the preferred host, and yield losses of between 15–73%
69 are typically caused by FAW outbreaks in corn.^{14, 15} Recent studies of projected yield loss
70 in Africa, combined across twelve major corn-producing sub-Saharan countries, indicated
71 that between 4.1–17.7 million tons of corn, with a value of \$1.09–4.66 billion, will be lost
72 annually due to the newly-invasive FAW populations.^{3, 4} China is the second largest corn
73 producer in the world, and corn is the third commonest crop after rice and wheat in China,
74 where it is grown in all provinces. The main corn-growing areas are the North China Plain
75 (mainly the provinces of Henan, Shandong and Hebei, see Fig. 1) and the Northeast
76 China Plain (Liaoning, Jilin and Heilongjiang, see Fig. 1) in eastern China, and these
77 regions (plus the Korean Peninsula and Japan) are potentially suitable for
78 summer-breeding populations¹³ if FAW can reach them. Therefore, Chinese agricultural
79 production and food security will be seriously threatened if FAW evolve a regular migratory
80 route which will allow them to exploit the principal corn-producing regions of East Asia to
81 the north and east of the current distribution.

82 International trade is considered to be an important cause of the rapid expansion of
83 FAW.¹³ In addition, this species has the capability to achieve natural long-distance range
84 expansion, as adults can migrate hundreds or even thousands of kilometres on
85 high-altitude winds over several successive nights;^{1,2} for example, FAW were reported to
86 be transported by low-level jets from Mississippi in the southern United States to southern
87 Canada, a distance of 1,600 kilometers.¹⁶ Although it is unlikely that natural windborne

88 migration was responsible for the moths crossing the Atlantic and Indian Oceans to
89 colonize Africa and India respectively, natural migration is hugely important for their spread
90 within Africa, and during their invasion of East and Southeast Asia.⁴ European countries
91 are worried about the very real possibility that the moths will migrate to Europe after they
92 breed successfully in North Africa.¹⁷

93 Now that FAW have arrived in Southeast Asia and southern China, there is a very high
94 possibility that they will invade eastern China on an annual basis. Two main migratory
95 routes are possible: a western and an eastern route. The western route involves
96 windborne transport from the westerly winter-breeding region (Myanmar / Yunnan), via
97 Guizhou and Sichuan and on into eastern China (Fig. 1). The eastern route originates from
98 the easterly winter-breeding region (northern Thailand, Laos, Vietnam, Guangxi and
99 Guangdong), and involves transport on favourable winds associated with movement of the
100 Asian monsoon via east-central China, and on into the main corn producing areas (the
101 North China and Northeast China Plains) (Fig. 1). The eastern route is the important
102 migratory pathway for many migratory pest moths in China, including beet armyworm
103 *Spodoptera exigua*,¹⁸ beet webworm *Loxostege sticticalis*,¹⁹ cotton bollworm *Helicoverpa*
104 *armigera*,²⁰ Oriental armyworm *Mythimna separata*²¹⁻²⁴ and rice leaf roller *Cnaphalocrocis*
105 *medinalis*.²⁵ As is the case for these other migratory pests, at these latitudes FAW can only
106 breed successfully in the summer and cannot survive overwinter, and so these regions will
107 need to be reinvaded on an annual basis.^{2, 13, 26} Hence, the question of whether FAW can
108 evolve a regular, seasonal round-trip migration between the year-round breeding zone in
109 Southeast Asia / southern China, and the potential summer-breeding zones in North and

110 Northeast China is the key to whether they can cause frequent and wide-scale crop
111 damage in China. However, East Asia would appear to be a very suitable region for the
112 development of long-distance annual migrations of FAW, for four reasons. Firstly, the
113 maize producing regions of eastern China lie at a similar latitude and have similar climate
114 to the FAW native migratory range in the USA. Secondly, East Asia has a wide extent of
115 tropical and subtropical regions on the Indochina Peninsula and in southern China, which
116 provide a favourable environment for FAW to maintain large populations over the winter.
117 Thirdly, there is a continuous agricultural ecosystem spanning a large latitude range in
118 Southeast and East Asia with year-round production of suitable crops (corn, sugarcane,
119 rice, etc) enabling continuous breeding if FAW can move between regions. Finally, the
120 annual East Asian summer monsoon provides a 'highway' of favourable winds for the
121 airborne transport of migratory organisms, towards the north in the spring and returning
122 south in the autumn. Taken together, this means the recent colonisation of Southeast Asia
123 and southern China is very likely to result in the emergence of a round-trip migratory cycle
124 that will exploit the seasonal resources available in eastern China. China is therefore
125 facing a great risk to its food security and agricultural productivity due to the invasion of
126 FAW into the region. It is thus important to identify the migration routes, timing of the
127 seasonal movements, and potential summer-breeding range of FAW in eastern China, in
128 order to design strategies to monitor and control this pest. In this study we predict the
129 future migratory pathways of FAW using trajectory simulations modified to take account of
130 FAW migration behaviour.

131

132 **2 METHODS**

133 We identified the potential endpoints of FAW moth migrations by calculating forward flight
134 trajectories from source areas where FAW are currently known to be breeding, or from
135 potential future source areas we predict they will breed in the near future. To improve the
136 accuracy of the trajectory simulations, we developed a new numerical trajectory model
137 that takes account of flight behaviour and self-powered flight vectors (as these are known
138 to substantially alter trajectory pathway^{27, 28}), and trajectory calculation is driven by high
139 spatio-temporal resolution weather conditions simulated by the Weather Research and
140 Forecasting (WRF) model.²⁹ This trajectory model has been used successfully for many
141 other insect migrants, such as corn earworm (*Helicoverpa zea*), Oriental armyworm, rice
142 leaf roller, and rice planthoppers.^{24, 25, 29-33} The program for calculating trajectories was
143 designed in FORTRAN^{24, 29, 31} and run under CentOS 7.4 on a server platform (IBM
144 system x3500 M4).

145

146 **2.1. Weather Research and Forecasting model**

147 The Weather Research and Forecasting (WRF) model (version 3.8, www.wrf-model.org)
148 was used to produce a high-resolution atmospheric background for trajectory calculation.
149 The WRF is an advanced meso-scale numerical weather prediction system
150 (<https://www.mmm.ucar.edu/weather-research-and-forecasting-model>).³⁴ In this study, the
151 dimensions of the model domain were 140 ×150 grid points at a resolution of 30 km.
152 Twenty-nine vertical layers were available and the model ceiling was 100 hPa. More detail
153 of the scheme selection and parameters for the modelling are listed in

154 Supplementary Table S1 and Fig. S1. National Centers for Environmental Prediction
155 (NCEP) Final Analysis (FNL) data was used as the meteorological data for the model input.
156 FNL is a six-hourly, global, 1-degree grid meteorological dataset. The model forecast time
157 is 72 h with data outputs at 1 h intervals, for horizontal and vertical wind speeds,
158 temperature and precipitation.

159

160 **2.2. Self-powered flight behaviours of FAW**

161 The flight behaviour of FAW were included in the trajectory simulation by making the
162 following assumptions. (i) Nocturnal moths perform 'multi-stop' migration, in which moths
163 only take off at dusk, terminate migratory flight the following dawn, and then take-off again
164 at the next dusk.^{25, 27, 28} FAW here was assumed to take off at 20:00 Beijing Time (BJT),
165 stop at 06:00 BJT, and fly for three consecutive nights whenever temperature conditions
166 were suitable (see below). (ii) Other species of similar-sized noctuid moth pests have a
167 self-powered flight speed of about 2.5–4 m/s.^{27, 35, 36} Therefore, we added a self-powered
168 flight vector of 3.0 m/s in the trajectory modelling. As we don't know if the Asian FAW
169 moths have a preferred flight heading, we assumed that the flight vector will be aligned
170 with the downwind direction. (iii) Radar studies of FAW in the USA^{1, 37-39}, and of similar
171 noctuid moth pests elsewhere^{27, 35}, show that these moths typically migrate at the altitude
172 of the of the low-level jet where wind speeds are relatively fast (often >10 m/s). We did not
173 explore altitudinal profiles of wind speeds before trajectory modelling, and thus to ensure
174 we would capture the most likely flight height, we started trajectories from eight different
175 altitudes: 500, 750, 1000, 1250, 1500, 1750, 2000 and 2250 m above mean sea level

176 (amsl). In the eastern pathway we only calculated trajectories at heights from 500–1500 m
177 amsl as ground heights in this region are relatively low, but we used all 8 altitudes for the
178 western pathway as much of the land in this region (particularly in Yunnan) is >1000 m
179 amsl. We assumed that FAW cannot fly when the air temperature at flight altitude falls
180 below 13.8 °C, the minimum temperature for survival of FAW^{13,40}, and so trajectories were
181 terminated on any night/height combination which dropped below this temperature.

182

183 **2.3. Departure points for forward trajectories**

184 We investigated the two main potential migratory pathways (the western and eastern
185 routes) by which FAW may annually invade eastern China, during four separate waves of
186 migration (March–April, April–May, May–June, and July). The western route originates in
187 Myanmar and Yunnan, and develops via Guizhou and Sichuan (Fig. 1). To model this
188 route, trajectories were started from all potential departure points at every 1° grid for the
189 following schemes: from (i) Myanmar and Yunnan in March–April; (ii) Yunnan in May; (iii)
190 Yunnan and Guizhou in June; and (iv) Yunnan and Guizhou in July (Fig. 2, Fig. S1).
191 Myanmar and Yunnan were selected due to the fact that FAW has been present during the
192 first winter period of 2019, and Guizhou was selected because many trajectories from
193 Yunnan reached this province in May.

194 The eastern route starts in northern Indochina, Guangxi and Guangdong, and
195 develops via east-central China towards the main corn-producing regions in North and
196 Northeast China (Fig. 1). To model this route, trajectories were started from all potential
197 departure points at every 1° grid for the following schemes: from (i) Thailand, and Laos /

198 Vietnam, in March–April; (ii) Guangxi and Guangdong in April–May; (iii) Hunan / Jiangxi,
199 and south Hubei / south Anhui, in May–June; and (iv) Hubei / Anhui, and Jiangsu /
200 Shandong, in July (Fig. 2, Fig. S1). The first two schemes were selected based on current
201 (April 2019) distribution of FAW, while the latter two schemes were selected based on the
202 results of the trajectories originating from the first two schemes earlier in the season.

203 We simulated the FAW trajectories by using average meteorological conditions at
204 flight altitude from the past 5 years (2014–2018). In total, >0.6 million trajectories were
205 calculated (Table S2), making this the largest study of FAW migration pathways
206 conducted.

207

208 **2.4. Effect of flight altitude on migration trajectories**

209 To investigate whether flight altitude would have affected distance and directional
210 components of the trajectories, we carried out a comparative analysis to see how three
211 migration parameters varied with altitude. Firstly, we calculated the average distance
212 travelled during the three nights of migratory flight at each of the modelled flight heights
213 (between 500 and 2250 m amsl in the western pathway, and between 500 and 1500 m
214 amsl in the eastern pathway), to see how distance varied with height across the regions
215 and seasons. Secondly, we looked at how the mean direction of the trajectories varied with
216 altitude. Thirdly, we investigated the degree of directional spread of the trajectories with
217 altitude. For each altitude, we used the Rayleigh test for circular data ⁴¹ to calculate the
218 mean direction and the r-value of the circular distribution of the directions of the trajectory
219 endpoints from the starting locations. The Rayleigh r-value ranges from 0 to 1, with higher

220 values indicating a greater clustering of directions around the mean and lower values
221 indicating a wider angular spread of trajectory endpoints. These three parameters
222 therefore indicate the effect that flight altitude selection will have on (i) the distance
223 travelled during migratory flights, (ii) the mean direction of windborne transport, and (iii) the
224 degree of dispersion or concentration that will occur over many nights of migratory flight.

225

226 **3. RESULTS**

227

228 **3.1. The Western Migratory Pathway**

229 The first detection of FAW in the East/Southeast Asian region occurred in Myanmar and
230 Yunnan (in the winter period of 2018/19)^{9, 10}, so we ran our first trajectories from these
231 areas during March–April. In both cases, the endpoints of these trajectories (the first wave
232 of migration) largely remained within Yunnan province indicating a rather slow northward
233 spread (Fig. 2). However, interestingly, some trajectories from Yunnan reached the
234 southeast corner of Guizhou province in this period, and this coincided precisely with the
235 location of a FAW outbreak discovered in late-April 2019.¹² The second wave of migration
236 moved much further from Yunnan, with many trajectories ending in Guizhou (Fig. 2) and
237 yet others travelling further east where they entered the eastern migratory pathway (see
238 below). During June (the third wave of migration), trajectories from Guizhou moved in a
239 northwards direction and FAW arrived in central China (eastern Sichuan, Chongqing and
240 southern Shaanxi). The fourth wave of migration during July took FAW into the more
241 easterly provinces of southern Shanxi, Henan and southern Shandong (Fig. 2). Our

242 trajectory simulations therefore show that FAW moths migrating along the western
243 pathway will reach the North China Plain during the fourth wave of migration (by July).

244

245 **3.2. The Eastern Migratory Pathway**

246 Migration trajectories originating from Thailand, and from Laos / Vietnam, during
247 March–April (the first migration wave) had a high probability of ending in southern China.
248 Trajectories from Thailand reaching China were concentrated mostly in Guangxi, while
249 those from Laos / Vietnam also had many endpoints in Guangxi, but in addition extended
250 further north and east, into most of Guangdong and also the southern parts of Hunan and
251 Jiangxi (Fig. 3). During the next stage of trajectories (the second migration wave),
252 modelled from Guangxi and Guangdong during April–May, FAW were predicted to
253 continue travelling further north and east into China, reaching the southern fringe of the
254 Yangtze River Valley. Guangxi trajectories were directed to the northeast and terminated
255 mainly in Hunan, but with many endpoints also in Jiangxi and the southern regions of
256 Hubei and Anhui (Fig. 3). Trajectories from Guangdong had a more easterly component,
257 and were concentrated in Jiangxi, Fujian and the southern part of Zhejiang (Fig. 3).

258 The third wave of migration was modelled from the Hunan / Jiangxi region, and the
259 south Hubei / south Anhui region, during May–June. The northward progression of the
260 migration continued in this period, although the distance travelled was relatively small and
261 trajectory endpoints were mostly concentrated in the region between the Yangtze and
262 Yellow River Valleys, in the provinces of Hubei, Anhui, Henan, Jiangsu and Shandong (Fig.
263 3). This partly overlaps with the important corn-growing region of the North China Plain

264 (Fig. 1). The fourth wave of migration during July involved a longer distance movement to
265 the northeast than in the third wave. Trajectories originating in Hubei / Anhui, and in
266 Jiangsu / Shandong, extended to the northern part of the North China Plain (Hebei), and
267 also reached important corn-growing regions in the Northeast China plain (Liaoning and
268 Jilin) and North Korea (Fig. 3). Our trajectory simulations therefore show that FAW moths
269 migrating along the eastern pathway will reach the North China Plain during the third wave
270 of migration (by June, that is a month earlier than the western pathway), and will then
271 reach the Northeast China Plain during the fourth wave (in July).

272

273 **3.2. Effect of flight altitude on migration trajectories**

274 In order to assess the role that flight altitude selection may have on migration pathways,
275 we analysed how distance, direction and degree of directional clustering of the trajectories
276 varied with altitude at each location (Fig. 4, Table S3). Trajectory height had a strong effect
277 on the distance travelled at some locations, but the direction of the trend with altitude
278 varied between sites, and in other regions there was no effect of altitude. In the western
279 flyway, early in the season most trajectories from Myanmar and Yunnan were
280 comparatively short irrespective of flight height (Fig. 4, Table S3) due to relatively cool air
281 temperatures, which explains why the initial northward spread from this region was rather
282 slow during March–April (Fig. 2). Later in the season however, as air temperatures
283 warmed, flight altitude had a large effect on distance travelled, with trajectories at
284 heights >1500 m producing considerably longer trajectories than lower altitudes in Yunnan
285 (typically 800–1000 km versus <500 km), but with the opposite trend in Guizhou where

286 flight below 1000 m produced the longest trajectories (Fig. 4, Table S3). Directions varied
287 with altitude in a complicated fashion across the different regions and time periods (Table
288 S3). The degree of directional clustering of trajectories tended to follow a regular pattern,
289 with tighter distributions occurring at high and low altitudes, but with a much greater
290 degree of dispersion at intermediate heights (Fig. 4).

291 Along the eastern pathway, trajectories tended to become longer and more tightly
292 clustered with increasing altitude in the Indochina Peninsula and southern China during
293 spring (Fig. 4). However, this patterns changed during late-spring and summer as the
294 moths moved further north into eastern China, with trajectory distance showing no pattern
295 with altitude but trajectory directions becoming more dispersed with increasing altitude in
296 the Yangtze and Yellow River Valleys and the North China Plain (Fig. 4). Once again,
297 directions varied in a complicated manner with altitude (Table S3).

298

299 **4. DISCUSSION**

300 In this study, we predicted future migration pathways of FAW in eastern China using a
301 trajectory analysis approach, combined with flight behaviour of FAW and meteorological
302 data from the past 5 years. Our results show that FAW will likely undertake annual
303 migrations from its new overwintering area in the Indochina Peninsula and South China
304 into the two main corn-producing areas of eastern China. The North China Plain (mainly
305 Henan, Shandong and Hebei) is predicted to be invaded in June each year after three
306 waves of migration along the eastern pathway, and then to receive another influx in July
307 due to a fourth wave of migrants coming from the western pathway. The Northeast China

308 Plain (Liaoning, Jilin and Heilongjiang) will then be invaded by a fourth wave of migrants in
309 July that originate for the population colonising North China a month previously. This likely
310 annual migration pathway will result in substantial damage and economic losses to corn
311 production in these two vitally important areas unless the FAW population can be
312 effectively managed.

313 Many species of insect carry out similar seasonal long-distance migrations in East
314 Asia⁴², including the most serious crop pests in this region, such as the oriental armyworm,
315 beet armyworm, cotton bollworm, rice leaf roller and rice planthoppers (*Nilaparvata lugens*
316 and *Sogatella fucifera*). Entomological radar studies have shown that the smaller,
317 relatively weak-flying species, such as the rice leaf roller and planthoppers, do not have
318 adaptive, wind-related, preferred flight headings or flight altitudes, and simply fly with
319 random orientation at the altitude where they reach their flight temperature threshold.⁴³⁻⁴⁵
320 This means these species will be passively transported downwind, with little or no
321 influence over their migration trajectories.^{42, 46} However, these weak-flying insects are still
322 capable of carrying out annual round-trip migrations between their winter-breeding regions
323 in Southeast Asia / South China, and summer-breeding regions much further north in East
324 Asia. This is because they can benefit from the seasonally-favourable winds that dominate
325 in this region, due to the passage of the East Asian monsoon.^{30, 47} This persistent
326 large-scale weather system produces frequent winds from the southwest in the spring and
327 summer, and then switches to frequent winds from the north in the autumn, over the entire
328 East Asian migration arena, thus providing suitable transporting flows for insect migrants
329 over the whole flight season.^{43, 47} Our study of likely FAW migration trajectories is entirely

330 consistent with this situation, and our modelling suggests that FAW only need to take-off
331 and climb to a few hundred meters above ground to achieve rapid, long-distance transport
332 towards eastern China during the spring. The migration system can therefore evolve
333 without any further specialised behaviours, simply due to the high frequency of
334 seasonally-favourable tailwinds. Presumably the progeny of the fourth wave will start to
335 return to the south from August onwards, though this idea still needs to be formally tested.

336 Simple reliance on seasonal patterns of suitable winds however is still a rather risky
337 and inefficient strategy, and more powerful fliers (such as noctuid moths) could
338 considerably improve the efficiency of their migratory flights, and reduce migration-related
339 mortality²⁸, by adopting beneficial flight behaviours. Radar studies of moth migration in
340 Europe^{35, 42, 48} have clearly demonstrated that a closely related species of migrant moth,
341 the silver Y *Autographa gamma*, has a syndrome of related behavioural traits which
342 significantly increase the speed, distance, directionality and success of its migratory flights.
343 These flight behaviours include the ability to detect and respond to the downwind direction,
344 restricting migration to nights with seasonally-favourable high-altitude tailwinds, selecting
345 the altitude with the fastest wind, and common orientation in seasonally-preferred
346 migration directions.^{42, 49-52} There is growing evidence that these behaviours are probably
347 widespread in larger insect migrants^{53, 54}, including Asian pest moths such as Oriental
348 armyworm and cotton bollworm.^{20, 21} It would thus seem very likely that FAW populations in
349 Asia will already have, or will rapidly evolve, some (or all) of these behaviours, and these
350 flight behaviours will have a major impact on their trajectories.

351 In our trajectories the only flight behaviour we encoded into our model was a

352 self-powered flight vector of 3 m/s in the downwind direction, whichever way the wind blew.
353 We did not allow moths to be selective of whether to migrate or not (depending on the wind
354 direction), nor did we allow them to orientate in seasonally-beneficial directions or select
355 flight altitudes based on wind speed. These decisions were made simply because we
356 know virtually nothing about the flight behaviour of the FAW populations in Asia, and we
357 felt it safer not to make too many assumptions for the purpose of this study. However, our
358 preliminary exploration of the impact some of these behaviours can have on migration
359 trajectories (see Fig. 4) clearly shows that an understanding of flight behaviour will be
360 crucial for accurately predicting the migration pathways and future range of this moth in
361 East Asia. Behavioural studies of FAW populations in southern China should thus be
362 carried out as a matter of urgency.

363 There are many similarities in the ecology and biology of FAW and Oriental armyworm,
364 including their migratory capability, body size and self-powered flight speed, wide host
365 range and pest status, and latitudinal extent of their breeding ranges, and thus it may be
366 assumed that the two species will have a similar migration pattern and phenology in East
367 Asia. The Oriental armyworm typically has only two steps in its northwards migration into
368 northeast China. The first step involves migration from its overwintering area south of the
369 Yangtze River into the plains between the Yangtze River and Yellow River (30°–35°N) in
370 March and April. The next generation then migrates as far north as Northeast China and
371 eastern Inner Mongolia, in a single step by May–June.^{22, 23, 55} However, our results indicate
372 that FAW will require three migration steps to reach the North China Plain in June, and four
373 steps to reach Northeast China in July. Thus its migration pattern is quite different from

374 that of the Oriental armyworm, presumably due to differences in their minimum
375 temperature for survival: 13.8°C for FAW, but only 9.6°C for Oriental armyworm.^{13, 40, 56} The
376 year-round distribution of FAW in East Asia is restricted to the relatively warm and moist
377 regions found on the Indochina Peninsula and in southern China (to the south of the Tropic
378 of Cancer)¹³, similar to rice planthoppers and the rice leaf roller.^{25, 46} Oriental armyworm
379 on the other hand can survive over winter in the region south of the Yangtze River (33 °N)
380 in China, considerably further north than FAW.⁵⁷ Due to their similar body size (and thus
381 flight capability and speed), and similar developmental periods (about one month per
382 generation under suitable temperature conditions), it is expected they will achieve similar
383 migration distances each year, and thus the occurrence area of FAW will be further south
384 than the Oriental armyworm at any one time.

385 The East Asian migration arena would appear to be a highly suitable environment for
386 the FAW, having suitable wind regimes for migration, suitable climate for rapid
387 development and widespread availability of corn. However, other factors may influence its
388 spread throughout the region, including distribution of alternative host plants, natural
389 enemies and competitors. The phenotype of FAW in Africa, Myanmar and Yunnan has
390 been identified as the corn strain, and the rice strain appears to be largely absent.^{25, 46}
391 However, as FAW populations arrive in South China, they will encounter large areas of rice
392 paddies, and relatively infrequent corn cultivation, which will affect its population growth.
393 Another factor which will determine population growth is the prevalence of natural enemies,
394 which may be expected to be low for a newly-invasive species. However, field surveys in
395 Yunnan found that 15–20% of FAW caterpillars were infected by parasitoid wasps

396 (unpublished data from G.P Li in Henan Academy of Agricultural Sciences), which is
397 encouraging from the perspective of population suppression via natural biological control.
398 In addition, FAW populations in East Asia will also encounter new competitors such as the
399 Oriental armyworm and the Asian corn borer *Ostrinia furnacalis*. None of these factors
400 were considered in our trajectory modelling, and we believe that ecological studies of FAW
401 populations as they colonise East Asia should be undertaken as a priority.

402 In conclusion, the major corn-growing regions of China face a high risk of invasion by
403 FAW. The North China and Northeast China Plains can be invaded by FAW via a series of
404 3–4 steps of northward migration, which will allow FAW to reach as far north as the border
405 of Jilin with Heilongjiang by July. The most efficient way to prevent invasive species from
406 entering a new country is efficient border quarantine. However, the ability of FAW to carry
407 out long-range, windborne migration means that traditional methods of surveillance and
408 quarantine are useless. When this study was began in January 2019, the FAW was only
409 known from Myanmar and Yunnan, and we wanted to know if it could invade the rest of the
410 Southeast and East Asian areas. In the intervening 4 months before this paper was
411 submitted in May 2019, FAW had already spread to Thailand, Laos, Vietnam, Guangxi,
412 Guangdong, Guizhou and Hunan, and its continuing spread through China to the north
413 and east seems inevitable. Additional studies on its migration patterns, flight behaviour,
414 ecology, and pest management are urgently required.

415

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425

426 **DECLARATION OF INTERESTS**

427 The authors declare that they have no competing interests.

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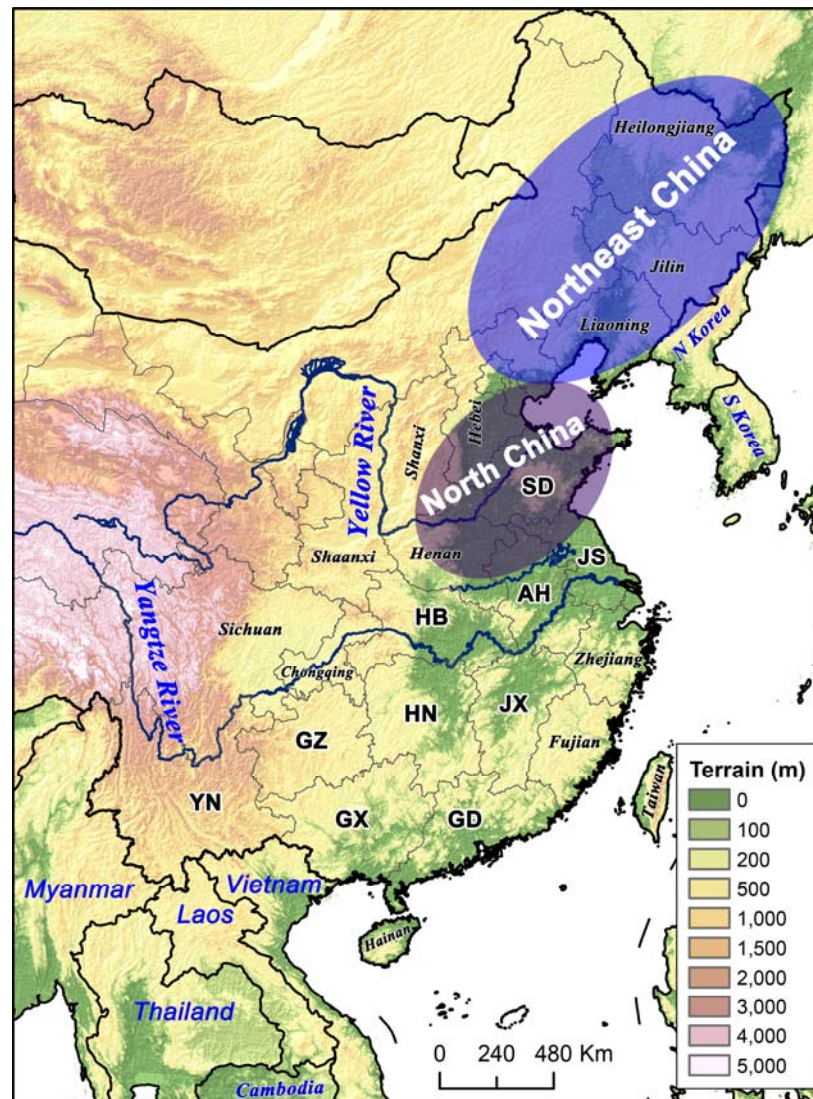
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622 **Figures**



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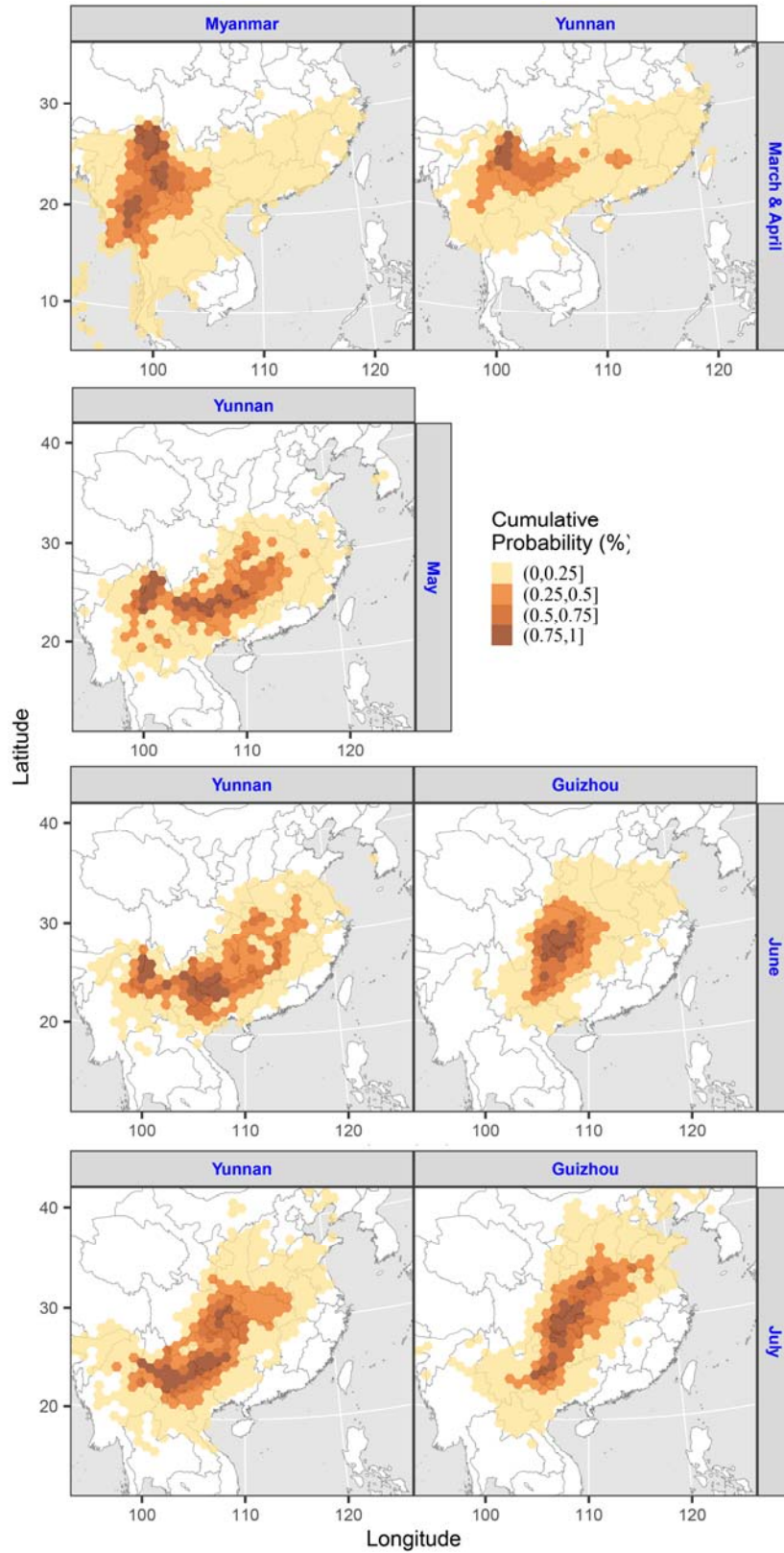
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625 **Figure 1.** Topography of the East Asian study area. Most of eastern China is a large area
626 of relatively flat land with few natural barriers to insect migration, but Southwest China
627 (Yunnan and Sichuan) is a largely mountainous area with many barriers to migration. Corn
628 is planted in each province in China, but the major corn-growing areas are the North China
629 Plain and the Northeast China Plain. Simulated migration trajectories of FAW were started
630 from Myanmar, Thailand, Laos, Vietnam and provinces in southwest, southeast and

631 east-central China indicated by a 2-letter code (YN: Yunnan, GX: Guangxi, GD:
632 Guangdong; GZ: Guizhou, HN: Hunan, JX: Jiangxi, HB: Hubei, AH: Anhui, JS: Jiangsu,
633 and SD: Shandong). Other provinces and countries mentioned in the text are indicated on
634 the map. The western migratory pathway originates in Myanmar and Yunnan, and passes
635 through Guizhou, Chongqing, Sichuan and Shaanxi before merging with the eastern
636 pathway. The eastern migratory pathway originates in northern Thailand, Laos, Vietnam,
637 Guangxi and Guangdong, and passes through all south-eastern and east-central
638 provinces before ultimately reaching the North China and Northeast China Plains.

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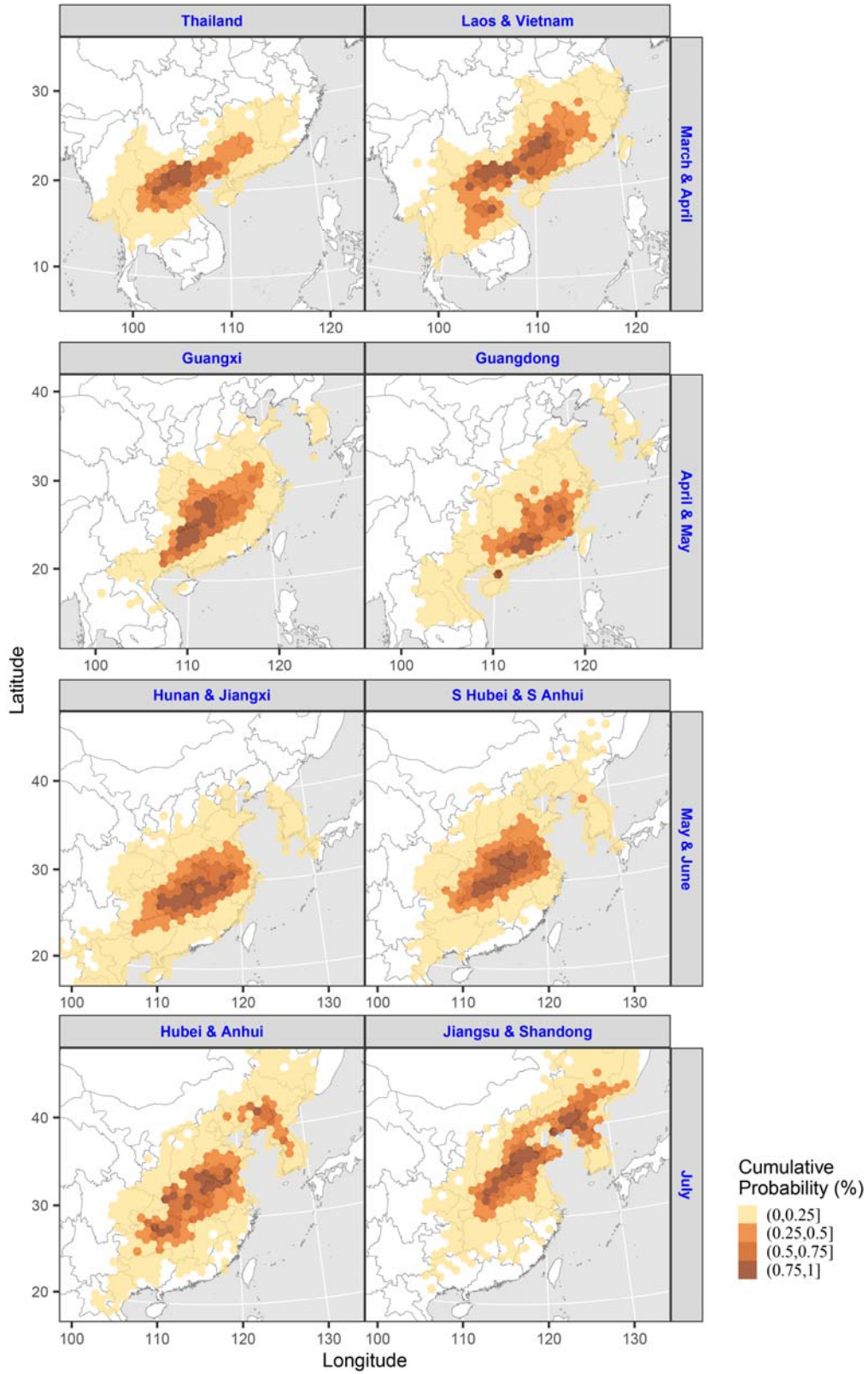
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643 **Figure 2.** Distribution of endpoints of FAW forward migration trajectories along the western
644 migratory pathway. The start-points and time periods of trajectories are labelled on the top
645 / right of each panel. Trajectory analyses were conducted over three consecutive nights,
646 and only the final endpoint of each 3-nights trajectory is shown. Each hexagonal cell
647 covers 10,000 km².

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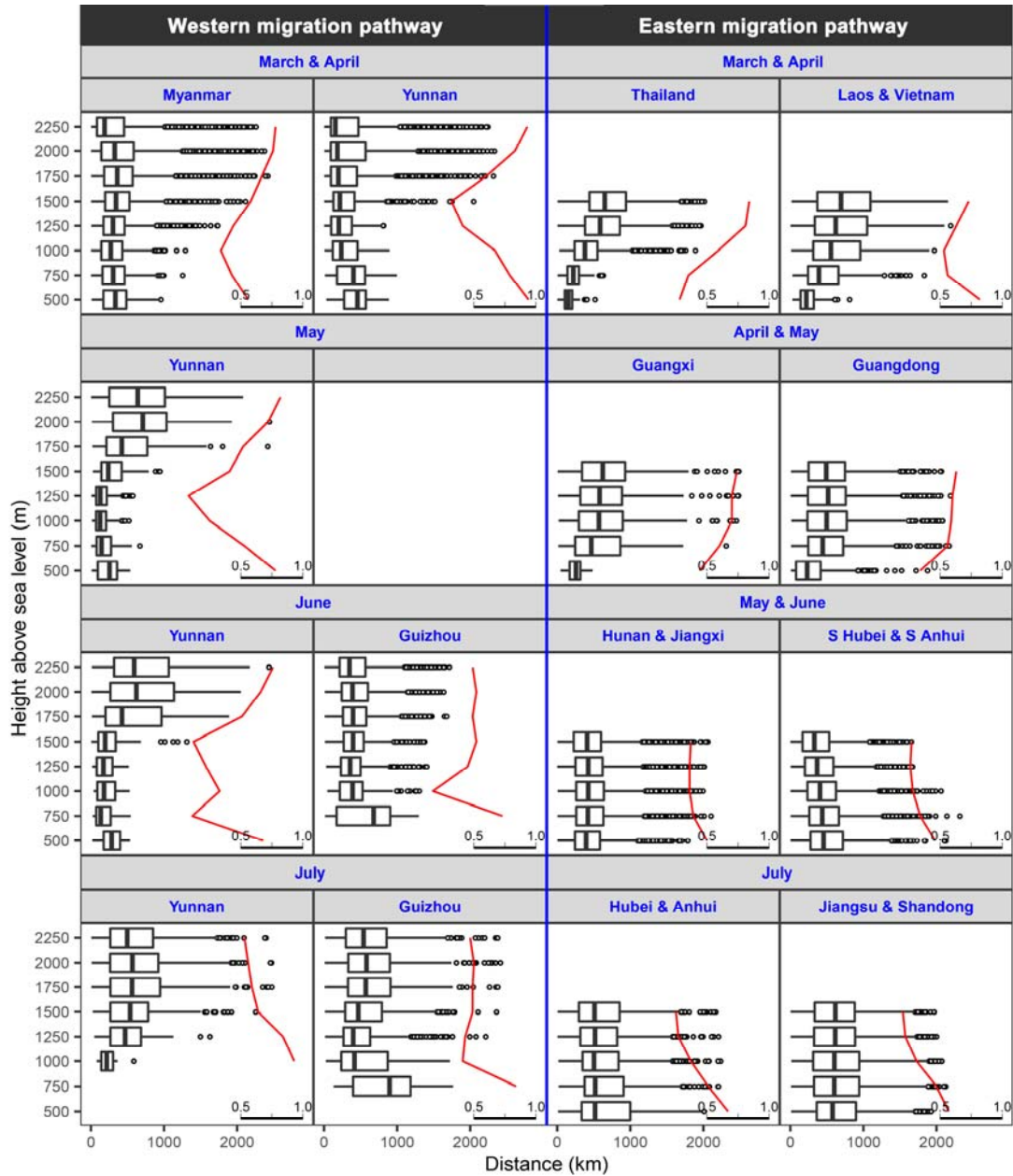
653 **Figure 3.** Distribution of endpoints of FAW forward migration trajectories along the eastern
654 migratory pathway. The start-points and time periods of trajectories are labelled on the top
655 / right of each panel. Trajectory analyses were conducted over three consecutive nights,
656 and only the final endpoint of each 3-nights trajectory is shown. Each hexagonal cell
657 covers 10,000 km².

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664 **Figure 4.** The effect of flight altitude on trajectory parameters. The black box plots show
 665 the straight-line distances between the start-points and the final endpoints for each
 666 trajectory, and how they vary with altitude. In the black box plots, central bars represent
 667 median values, boxes represent the inter-quartile range (IQR), whiskers extend to
 668 observations within ± 1.5 times the IQR, and dots represent outliers. The red lines (on a

669 secondary scale) show the Rayleigh test r -values for the trajectory directions at each
670 altitude. This provides a measure of the degree of clustering of the angular distribution of
671 directions around the mean, ranging from 0 to 1, with higher values indicating tighter
672 clustering and thus a higher degree of common trajectory directions and lower values
673 indicating a greater dispersion of trajectories.

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