

Multilevel climatic responses in migratory insects

Edit Juhász¹, Zoltán Németh^{1, 2}, Ádám Górh³, and Zsolt Végvári^{4,5}

¹Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Egyetem tér 1, Hungary

²ELKH-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Egyetem tér 1, Hungary

³Department of Ecology, University of Veterinary Medicine, Budapest 1077, Rottenbiller u. 50., Hungary

⁴Institute of Aquatic Ecology, Centre for Ecological Research, Karolina u. 29, H-1113, Budapest, Hungary

⁵Senckenberg Deutsches Entomologisches Institut, D-15374, Müncheberg, Germany

Running head: Climatic effects on migratory insects.

Key words: climatic responsiveness, climatic scales, migratory insects, ecological predictors

23

24

25 **Abstract**

26

27 Evidence is mounting that migration in ectotherms is more widespread than formerly believed.

28 Thus, a number of insects living in temperate climates, including locusts, butterflies, moths and

29 dragonflies following seasonal migration strategies show high responsiveness for alterations in

30 climatic processes, similarly to a broad taxonomic range of birds. On global scales, migratory

31 insects include iconic large butterflies, dragonflies and also a number of crop pests. However, insect

32 migrations are ecologically distinct from those of vertebrates, often relying heavily on seasonal

33 winds and multiple generations to complete a full annual cycle, due to short insect life spans.

34 Here we review publicly available online resources to identify key patterns of spatial, taxonomic

35 scales and complexity of climatic responsiveness to environmental predictors in migratory insects.

36 We found that migratory insects respond to various levels of complexity in climatic patterns and

37 these responses are predicted by life history and ecological traits: i) responses to climatic effect type

38 was predicted by climate zone(s) of the distribution area, whereas ii) response to climatic

39 complexity was predicted by body size. In conclusion, migratory insects respond to various levels

40 of complexity in climatic processes and this responsiveness is governed by a substantially wider

41 array of environmental predictors than demonstrated in vertebrates.

42

43

44 **Introduction**

45

46 During the past decades, an increasing number of investigations revealed that migration - when

47 individuals regularly travel between the breeding and non-breeding areas along directed paths - is a

48 key life history trait not only in birds and mammals, but also in ectotherms, such as insects and
49 crabs (Rainey 1963; Schaefer 1969; Urquhart & Urquhart 1978; Dingle 1996). On global scales,
50 migratory insects include iconic large butterflies (e.g. *Danaus plexippus*), dragonflies (e.g. *Pantala*
51 *flavescens*) and also a number of crop pests (e.g. *Agrostis ypsilon*) (Holland *et al.* 2006; Chapman *et*
52 *al.* 2015). Moreover, other less conspicuous groups of insects have also been shown to migrate,
53 such as hoverflies (Wotton *et al.* 2019) and aphids (Bell *et al.* 2015). Insect migrations are
54 ecologically distinct from those of vertebrates, often making use of seasonal winds and relying on
55 multiple generations to complete a full annual cycle, due to short insect life spans (Chapman *et al.*
56 2011).

57 Seasonal migrations of insects vary widely in their spatial patterns (Satterfield *et al.* 2020),
58 encompassing both the well-known round-trip migrations of numerous hoverfly, dragonfly, and
59 butterfly populations, including the Monarch Butterfly (*Danaus plexippus*) and the Painted Lady
60 (*Vanessa cardui*) (Chowdhury *et al.* 2021; Stefanescu *et al.* 2007, Stefanescu *et al.* 2013, Hu *et al.*
61 2021), as well as the more complex movements of Desert Locusts (*Schistocerca gregaria*, Kennedy
62 1951) and Australian Armyworm Moths (*Mythimna convecta*, Farrow & McDonald 1987),
63 migratory journeys of which form interconnected networks across continents. Other insects like
64 Mustard Aphids (*Lipaphis erysimi*) and Green Lacewings (*Chrysoperla carnea*) demonstrate
65 seasonal migrations radiating out from source sites, resulting in repeated population-scale patterns
66 (Drake & Gatehouse 1995).

67 Studies revealed that several insects (e.g. Oleander Hawkmoths [*Daphnis nerii*] in Japan; Ohba *et*
68 *al.* 1999) are altering the phenology or topological properties of their seasonal movements in
69 response to environmental change. Moreover, some migrants have already shifted their ranges
70 northwards (Satterfield *et al.* 2020) as a response to warmer temperatures (Sparks *et al.* 2005). For
71 example, Juhász *et al.* (2021) found that the relative intensity of the first and last migratory peaks of
72 the Painted Lady significantly increased and showed temporal advancement during the past decade.

73 Migratory insects may be especially vulnerable to current global climatic trends, owing to their
74 dependence on spatially distributed resources, which may be differentially influenced by changes in
75 climate (Lemoine & Böhning-Gaese 2003; Oberhauser & Townsend Peterson 2003). For example,
76 the Cloudless Sulphur (*Phoebis sennae*) and Question Mark (*Polygonia interrogationis*) butterflies
77 in the US (Breed *et al.* 2013), as well as the Giant Honeybee (*Apis dorsata*) in India (Sihag 2014)
78 show marked climatic responsiveness mediated by the distribution of their food plants. Similarly,
79 even the once highly abundant Rocky Mountain Locust (*Melanoplus spretus*) has been shown to be
80 driven to the verge of extinction by adverse environmental processes: this locust once performed
81 dry-season migrations in invasion-like numbers from high-altitude to low-altitude zones in the
82 Rocky Mountains (Sorensen 1995). Additionally, once widespread macro-moths (including pests)
83 are also declining in the UK, including the migratory Silver Y (*Autographa gamma*), Black
84 Cutworm (*Agrotis ipsilon*), and Turnip Moths (*Agrotis segetum*) (Fox 2013). Indeed, climate change
85 has been confirmed to modulate the dynamics of migratory insect populations (Fox *et al.* 2014,
86 Conrad *et al.* 2004).

87 A key component of analysing how changes in climate impact the migration strategy of various
88 species is the identification of the most influential climatic parameters. Theory predicts that
89 migratory species will vary in their sensitivity to meteorological conditions and that this
90 responsiveness may be time-dependent and may change over the range of the species (Robinson *et*
91 *al.* 2005). Further, insects' responses to climatic conditions have been shown to vary on the levels
92 and scales of climatic processes: climatic responsiveness might be dependent on i) causal
93 mediation, defined as direct (i.e. the response is strongly correlated with the climatic parameters) or
94 indirect (i.e. the response is not related directly to climatic processes but strongly correlated with an
95 ecological process or pattern which is governed by climatic trends) effects; ii) spatial scale, defined
96 as local (i.e. confined to a region) or continental (i.e. covers at least 50% of a continent); and iii)
97 complexity, classified as responses to a single or multiple climatic parameters or composite

98 processes, such as atmospheric circulations (Boggs & Inoyue 2012; Boggs 2016; Forrest 2016;
99 Halsch *et al.* 2021).

100 To explain the climatic responsiveness of insects, several studies have shown the importance of a
101 number of life history attributes (Robinet & Roques 2010; Halsch *et al.* 2021). In migratory insects,
102 body size is predicted to be influential for climatic responsiveness as body metrics are key drivers
103 of migratory performance in insects (Dingle *et al.* 1980, Rankin & Burchsted 1992, Hu *et al.* 2018).
104 The wintering stage has been shown to govern climatic responsiveness in lepidopterans. For
105 example, a former study of ours has demonstrated that nocturnal moths (Noctuidae) hibernating as
106 adults shift their time of emergence to earlier dates than species spending the winter as eggs, larvae
107 or pupae (Végvári *et al.* 2015, Altermatt 2010).

108 Apart from life history traits, a broad range of ecological and life history metrics of insects in
109 general has been shown to be influential for climatic responsiveness, such as the number of
110 generations per year, habitat association, overwintering strategy and responsiveness to specific
111 climatic parameters (Halsch *et al.* 2021). Several investigations found that climate zone is a
112 potential predictor of climatic responses in migratory insects, as the different climatic zones of the
113 earth are differentially affected by climate change, inducing non-analogous processes in ecological
114 networks (e.g. Woodward *et al.* 2010, Musolin & Saulich 2012).

115 Although migratory insects exhibit immense taxonomic diversity and high variance in migration
116 strategies, our knowledge of the environmental responsiveness of migratory strategies are extremely
117 limited due to the lack of quantitative and long-term datasets.

118 Thus, the aim of our study is to summarise the current state of knowledge on insect migration in
119 relation to climatic processes. Our review is organised around the following research questions: (1)
120 What are the levels of climatic complexity influencing behavioural responses of migratory insects?
121 (2) Which life history traits influence climatic responsiveness?

122

123 **Methods**

124

125 *Literature search*

126 We searched for research articles on insect migratory behaviour in connection with climatic
127 changes. We used the Scopus (www.scopus.com) database to generate a list of papers based on the
128 following search terms: ‘insect’ and ‘migration’ and ‘clima*’ including all papers published prior to
129 June 2023, and expanded this list by searching for articles on known migratory species in Google
130 Scholar.

131 As a result, we found 446 papers matching the search terms. Using the abstracts, we narrowed down
132 the list by excluding papers which only generally referred to relationships among migration and
133 climate in insects, which resulted in a subset of 230 papers. Moreover, we also considered the
134 migration type of the species during the selection of the papers for the analyses: we used only
135 papers which considered seasonal migration (particular stages of annual journeys, following the
136 recommendations of Dingle (2007)). Thus, dispersion and other types of movements among close
137 populations were not considered as migration in this study. Finally, our search yielded 76 papers
138 matching our criteria. In the next step, we divided these papers into two subsets: i) review articles
139 providing additional general information on insect migration related to climate, which we excluded
140 from further analyses as these lacked species-specific data and ii) research papers based on species-
141 specific investigations on climatic responsiveness. We used the research papers to obtain data for
142 further analyses.

143

144 *Data analyses*

145 First, we quantified the following metrics: number of papers from different years, number of
146 investigated insect groups and geographic locations of the studies. Studies on the insects’ responses
147 to climatic processes were classified as those related to phenology or demography. As we found

148 only three studies analysing demographical responses, we omitted these from further analyses,
149 focusing only on the potential drivers of phenological response. In total, we used 57 papers in the
150 further analyses (Appendix 1.) During paper search, selection and data retrieval, we included all
151 species-specific records, irrespective of level of significance.

152 In the next step, we created a database with the following response and proxy variables retrieved
153 from papers. First, for each species we classified the climatic parameters which predicted a
154 response, considering relationships between insect response and climatic predictors found in the
155 original papers, independent of the level of significance (significant or not). Based on the array of
156 dependent variables treated in the papers, in the next step, we classified the climatic responses into
157 three main groups, using the species-level subsets of climatic parameters which relate to various
158 levels of reactions to climatic complexity: response to i) the directness of the climatic parameter,
159 classified as direct or indirect; ii) geographic scale of the climatic parameter, defined as local or
160 continental and iii) complexity of the climatic response, defined as single, multiple, complex:
161 “single” is assigned to species reacting to a single climatic parameter, “multiple” response indicates
162 a reaction to several climatic parameters on local scales within the same study, referring to the same
163 species, whereas “complex” indicates responsiveness to composite climatic patterns, such as
164 atmospheric circulations, also within the same study (Appendix 2.) As potential predictors of these
165 response variables, we considered i) body size (measured as wingspan in butterflies, provided as
166 body length otherwise, provided in mm-s), which is widely accepted as a proxy of a large number
167 of life history variables across the animal kingdom; ii) wintering stage was categorized as adult,
168 egg, larva, or pupa; iii) climate zone describing the major climatic zones intersecting the
169 distribution range, retrieved from taxon-specific literature and online databases (C FC Lt. Fraser
170 1936; Needham 2000; CABI 2022, GBIF.org 2022, Jonko 2022).

171 As the study species are distributed over a broad taxonomic range of insects, we controlled
172 for phylogenetic non-independence of the taxa by collecting order-level taxonomic information on
173 the studied insects, as provided by the original papers.

174

175 *Statistical analyses*

176 We calculated the variance inflation factors (VIF) between all predictors to test for multicollinearity
177 using the 'usdm' package in R. The VIF-values for all of the predictors were found to be < 1.30,
178 thus considered as weakly correlated. As the next step, we fitted Generalised Linear Mixed Models
179 (GLMM-s) on the i) climatic effect type (direct or indirect), ii) climate scale and iii) climate
180 complexity as response variables, as a function of log-transformed body size, climate zone and
181 wintering stage, treating study ID and insect order as random factors and considering binomial error
182 family. We entered insect order as a random factor because this is recommended as a surrogate
183 method for controlling for phylogenetic dependence without having a phylogenetic tree of finer
184 resolution (Chamberlain et al. 2012).

185 In the next step, we conducted a model selection procedure, considering each of the three
186 models as full models separately, employing climatic effect, climatic scale and climatic complexity
187 as response variables in the separate models. In the case of the weather complexity that has three
188 levels, the 'glmer' package of the R statistical environment allows the use multi-level categorical
189 response variables, thus performing multinomial regression; statistically, the three-level categorical
190 response variable is treated as if it were a set of independent binary responses where each level of
191 the response variable is considered a "success" with a certain probability, and the goal of the
192 modelling is to model the probability of each level occurring as a function of the predictor variables
193 'lme4' package (Bates *et al.* 2015). After model fitting, the relative importance of life history traits
194 (body size, wintering stage) and climate zone of distribution was calculated using information-
195 theoretic model-comparison, considering all candidate models, which in our case meant the

196 formulation of 8 candidate models for each response variable (Appendix 3.) Burnham and Anderson
197 2002). First, we obtained the values of Akaike's information criterion corrected for small sample
198 size (AICc) and the corresponding Akaike weight of each model (ω). Second, calculated model-
199 averaged parameter estimates (β), unconditional standard errors (SEu; Burnham and Anderson
200 2002), z-value of z-approximation and related p-values of each variable by the sums of their Akaike
201 weights across all models. Akaike differences in the range 0–4 indicate substantial level of
202 empirical support of a given model, whereas $\Delta_i = 7$ implies very weak support (Burnham and
203 Anderson 2002).

204

205 GLMM-s were fitted applying the 'glmer' function available in the 'lme4' package (Bates *et al.*
206 2015) and model selection was carried out applying the 'MuMIn' package (Barton 2020); all of the
207 packages are provided within the R Statistical Programming Environment (R Core Team 2022).

208

209 **Results**

210

211 *Primary database*

212 Our dataset, compiled from 57 papers, consisted of records of 61 insect species classified into five
213 insect orders, where each species occurred 1-5 times in the analysed investigations and the number
214 of species ranged between 2 – 34 in the insect orders (Fig 1, Appendix 2). The 57 original papers
215 contained information for altogether 61 species, where several papers provided data for more than
216 one species, which thus provided the 84 rows of the appendix table showing the original data
217 (Appendix 2). The species in our study originated from five climate zones, where the number of
218 species ranged between 10 – 17 in the various climate zones (Fig 2., Appendix 2). The studied
219 species originated from all continents with the exception of Antarctica and the number of species
220 per continent varied between 1 – 25 (Fig 3., Appendix 2). Considering the levels of significance of

221 the climatic relationships reported in the papers, we found five studies that also reported non-
222 significant results and only a single one reporting exclusively non-significant relationships; the
223 subset of papers providing non-significant results referred to 10 species. However, the type of
224 climatic response for the same metrics we applied for significant results (climatic effect, climatic
225 scale and climatic complexity) was found to be constant; thus, due to the lack of variation for the
226 studies with non-significant results, we could not include “level of significance” as a factor in the
227 analysis.

228

229 *Climatic drivers*

230 Among the investigated climatic predictors, four key parameter groups emerged: temperature,
231 precipitation and predictors describing the dynamics of the atmosphere, such as atmospheric
232 pressure, wind and weather systems (Mak 2011). Out of these, temperature was demonstrated to be
233 the most dominant climatic parameter, acting both directly and indirectly on climatic responsiveness
234 of phenological patterns for the largest number of study species, distribution areas and trophic
235 networks. For example, a study on the Northern Californian breeding population of the Monarch
236 Butterfly reported a positive influence of warmer temperatures on the probability of Monarch
237 presence in the breeding area (Lemoine 2015); however, the findings of that study indicate that host
238 plant distributions predict Monarch distributions to a higher degree than climatic metrics. Similarly,
239 Lemoine (2015) found that the ranges of both the Monarch and its food plant appear to be
240 constrained by temperature, whereas the distribution of the host plant explains the majority of the
241 variability found in Monarch observations. Another example of climatic influences mediated by
242 host plant responsiveness to temperature changes is shown by aphids, for which the spring
243 migration phenology has shifted in parallel to winter and early spring temperatures (Luquet *et al.*
244 2019). Direct temperature effects on population-level responses to climatic variability have been

245 found in the noctuid moth *Autographa gamma*, the population sizes of which are closely related to
246 winter temperatures of the overwintering areas (Chapman *et al.* 2012).

247 Wind is an environmental driver that has increasingly been demonstrated to be highly influential for
248 climatic responsiveness of migratory animals. For example, the migratory flights of the moth
249 *Spodoptera frugiperda* are predominantly predicted by the speed and direction of wind (Westbrook
250 *et al.* 2019). Similarly, shifts in wind direction and speed as a result of current climatic processes
251 have been demonstrated to modulate migration routes of Desert Locusts as these insects are passive
252 fliers (Cressman 2013).

253 Considering correlations between migration strategy and climate, in 40 % of the papers we found
254 direct relationships between the climatic variables and migration. For example, atmospheric
255 circulations have been shown to play roles in the climatic responsiveness of *Nilaparvata lugens* and
256 several *Spodoptera* species, whereas temperature was found to be the key predictor of climatic
257 responses of *Autographa gamma* and several *Spodoptera* species (Westbrook *et al.* 2019,
258 Torniainen & Mikonranta 2018, Hu *et al.* 2019). In the other 60 % of the selected papers, we
259 detected only indirect connections, which were mainly linked to food plant phenology in response
260 to climatic changes. During the detailed analysis we uncovered that the indirect effect of climatic
261 changes was detected mainly (70% of N=18 studies) in lepidopterans.

262
263 *Associations among climatic responsiveness, life history and ecological predictors*

264 As the model selection procedure performed on the full generalised linear mixed models requires a
265 dataset without missing values, the omission of records where at least one ecological or life history
266 predictor was lacking – which happened in several cases – the sample size correspond to the
267 number of records of the filtered dataset, which is 72 in our analyses. The directness of the climatic
268 effect was predicted by climate zone(s) and marginally significantly by body size: species
269 distributed in regions with temperate as well as tropical climates were largely indirectly influenced

270 by climate parameters, whereas insects with distribution areas in colder regions responded more
271 strongly to direct effects (model-averaged GLMM, $N = 72$, $b = -27.5318$, $p = 0.045$; Table 1, Fig
272 4); larger-bodied insects tended to respond more to indirect climatic effects, whereas smaller species
273 were more responsive to direct climatic effects (model-averaged GLMM, $b = 14.0235$, $p = 0.0389$;
274 Table 1, Fig 5, Appendix 3).

275 Climatic complexity was strongly associated by body size: with decreasing body size, insects were
276 increasingly responsive to multiple climatic patterns, reacting increasingly strongly to simple and
277 complex patterns (model-averaged GLMM, $N = 72$, $b = 8.7468$ $p = 0.0003$; Table 2, Appendix 3).

278 Climatic scale was unrelated to any of the model predictors (body size, wintering stage and climate
279 zone; model-averaged GLMM, $N = 72$, $p \geq 0.9478$ for all cases; Table 3, Appendix 3).

280 The phylogenetic signal in the global model measured as the variance of the insect order treated as
281 random term was found to be low: $S^2 \pm SD = 8.58 \pm 2.929$.

282

283 **Discussion**

284

285 Our key findings indicate that migratory insects respond to various levels of complexity in climatic
286 patterns and these responses are predicted by life history and ecological traits: i) responses to
287 climatic effect type were predicted by climate zone(s) of the distribution area, whereas ii) response
288 to climatic complexity was predicted by body size. We discuss these relationships in detail.

289 Our result that species distributed in regions with colder climates responded more to direct effects
290 than insects with distribution areas in warmer regions can be explained by the following, mutually
291 non-exclusive hypotheses. First, climatic processes are less complex in the cold and/or temperate
292 and arctic zones than in the temperate and/or tropical regions (Lydolph & Temple 1985), which is
293 thus predicted to select for responsiveness to direct climatic effects in insects. Alternatively, the
294 annual activity period of insects distributed in colder regions is substantially shorter and constrained

295 to the warmer months of the year than those occupying hotter climatic zones which induces the
296 emergence of more direct responses to weather parameters such as temperature changes. For
297 example, spring emergence in many species are driven by direct climatic cues (Boggs 2016).

298 Our finding that larger-bodied insects were more responsive to multiple local climatic patterns,
299 whereas smaller-bodied species reacted more to both simple and complex local patterns invokes
300 two mutually non-exclusive hypotheses. First, the decreased ability of smaller-bodied insects to
301 perform active migratory movements in the air as compared to larger insect predicts that species
302 with smaller body size and migratory ranges are more responsive to simple climatic parameters than
303 to complex ones. Alternatively, smaller species migrating on continental scales may benefit from
304 evolving navigation senses using complex environmental cues leading to optimised navigation
305 decisions (Aralimarad *et al.* 2011). Indeed, larger insects perform better in active flight; one of the
306 hypotheses explaining this pattern states that larger insects are less dependent upon evolving
307 navigational mechanisms supporting passive flight mechanisms, which might be highly important
308 for the survival of smaller insect species during migration (Menz *et al.* 2022). However, to test these
309 hypotheses, we need to have more data on the migration distances of the studied species.

310 The number of research papers analysing relationships among insect migration and climatic
311 processes has been growing in the past few decades, deepening our knowledge on the
312 environmental background of migratory mechanisms in ectotherms. This is facilitated by the fast
313 accumulation of information on climatic changes during this period. We found that the majority of
314 the papers in consideration confirm that migratory behaviour in insect species is impacted by
315 climatic processes, however, the causal relationships among the underlying mechanisms are still far
316 from understood. Further, a significant component of the complexity of determining how changes in
317 climate may impact migratory species is driven by the identification of the potential climate
318 variables which are most relevant to the biology of the given species. Indeed, insects are sensitive to
319 particular meteorological conditions to various degrees and this sensitivity may vary over time

320 (including various aspects of their life cycle) and across the range of the species (Chambers 2009).
321 Furthermore, interspecific differences can also be detected in sensitivity to environmental factors
322 such as temperature, therefore warming can increase or decrease synchronization between insects
323 and their food plants and/or natural predators (Forrest 2016).

324 Considering the investigated climatic predictors, temperature was the most commonly studied
325 climatic parameter, which affects migration in different ways. For example, Bradshaw & Holzapfel
326 (2010a, b) investigated the geographical and seasonal patterns in light and temperature in the
327 temperate zone, and how climate change influences migration patterns and the actual and potential
328 biotic responses by insects to climate warming. They found that across a large taxonomic range,
329 each individual shows genetically driven responses to temperature, which induce irrevocable
330 physiological decisions whether to initiate migration or not. Future environmental conditions then
331 determine the fitness consequences of that decision. Specifically, physiological processes drive
332 functional relationships between the genotype and the phenotype that ultimately confronts the
333 environment and influences individual fitness. As wild animals face environmental variability and
334 cope with that variation through physiological adjustments at the behavioural, hormonal, cellular,
335 and biochemical levels.

336 Considering response variables, we found that phenological shifts were the most commonly found
337 reaction to climatic changes. Related studies indicate that changes in phenology can influence
338 species interactions (including pollination), population viability, water cycles, carbon sequestration,
339 human health (allergenic disorders, vector borne diseases, pest insect control), tourism and
340 recreation, transport (e.g. bird migration and aircraft collisions), timing of management activities
341 and productivity in agriculture (Chambers 2009). Given the often strong relationships between
342 changes in climate and changes in phenology, phenological measures can also be used as proxies for
343 climate change. Most of the knowledge about changes in phenology comes from the Northern

344 Hemisphere mainly from Europe alone (Chambers 2009) limiting our understanding of the diversity
345 of organismal response to climate change.

346 Numerous effects of climate change on spring phenology of plants and animals have been
347 documented (Wolkovich *et al.* 2012; Parmesan *et al.* 2013). We also noticed that in investigations
348 analysed in our study, the changes in insect phenology were always monitored in spring.
349 Interestingly, autumn seemed to be a neglected season in climatic studies conducted in temperate
350 and arctic ecosystems. A recent study analysing this pattern (Gallinat *et al.* 2015) showed that leaf
351 senescence and bird migration are the most frequently examined responses in autumn, and insect
352 diapause and fruit ripening have so far received only moderate interest.

353 Our study might be biased by the latitudinal distribution of study locations, as the majority of the
354 investigations have been conducted in the Northern Hemisphere, which tendency is also found in
355 avian studies of climatic responses (Dunn & Moller 2019). This calls for a more active sampling at
356 southern latitudes which might be important for outlining management plans for endangered
357 species. Additionally, the publication bias towards publishing mostly significant results – also found
358 in our study – might affect the results of meta-analyses, which has also been reported in ecological
359 studies (Lortie *et al.* 2007). To overcome this problem, we encourage ecologists to publish non-
360 significant results, which is expected to deepen our understanding of fundamental ecological issues.

361 We also detected several knowledge gaps in climatic investigations of migratory insects, which
362 when addressed would substantially contribute to clarifying some causal mechanisms. Out of these,
363 we emphasise the small number of studies i) analysing relationships among physiological
364 adaptation to migration and climate and ii) the genetic and epigenetic background of climatic
365 fingerprints in migratory behaviour.

366 Finally, we recommend to investigate the so far underestimated effects of changes in a wider range
367 of potential environmental predictors such as climatic teleconnection networks – defined as large-
368 scale atmospheric and oceanic interactions that link different regions of the Earth's climate system,

369 which involve the exchange of energy, moisture, and momentum between distant locations,
370 influencing weather patterns and climate variability on a global scale – solar radiation, humidity,
371 and levels of greenhouse gases, which are expected to modulate climatic responsiveness in
372 migratory insects (Robinet & Roques 2010). Climatic extremities also need more focus in climatic
373 ecology, as the increasing frequency of arid periods, storms, extreme cold events in spring and heat
374 shock days have already been shown (Forrest 2016) to exert strong effects on insect migration, by
375 blocking or altering migration routes.

376 To conclude, we show that migratory insects respond to various levels of complexity in climatic
377 processes, and this responsiveness is i) predicted by life history and ecological proxies; and ii)
378 governed by a substantially wider array of environmental predictors than demonstrated in
379 vertebrates.

380

381 **Acknowledgements**

382

383 On behalf of Project ‘TetraClim’, we thank for the usage of ELKH Cloud (<https://science-cloud.hu/>)
384 that significantly helped us achieving the results published in this paper. Hereby we declare that
385 none of the authors of the present work are involved in any type of conflict of interest affecting the
386 current research. Z.N. was supported by the National Research, Development and Innovation Office
387 of Hungary [FK 124414], the János Bolyai Research Scholarship, and the ÚNKP-21-5 New
388 National Excellence Program of the Ministry for Innovation and Technology from the source of the
389 National Research, Development and Innovation Fund.

390

391 **References**

- 392 Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths.
393 *Proceedings of the Royal Society B: Biological Sciences*, **277(1685)**, 1281-1287.
- 394 Aralimarad, P., Reynolds, A.M., Lim, K.S., Reynolds, D.R. & Chapman, J.W. (2011) Flight altitude
395 selection increases orientation performance in high-flying nocturnal insect migrants. *Animal*
396 *behaviour*, **82(6)**, pp.1221-1225.

- 397 Bartoń, K. (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
398 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 399 Bates, D., Maechler, M., Bolker, B. & Walker S. (2015) Fitting Linear Mixed-Effects Models Using
400 lme4. *Journal of Statistical Software*, **67(1)**, 1-48. doi:10.18637/jss.v067.i01.
- 401 Bell, J. R., Alderson, L., Izera, D., Kruger, T., Parker, S., Pickup, J., ... & Harrington, R. (2015).
402 Long-term phenological trends, species accumulation rates, aphid traits and climate: Five
403 decades of change in migrating aphids. *Journal of Animal Ecology*, **84(1)**, 21-34.
- 404 Boggs, C.L. & Inouye, D.W. (2012) A single climate driver has direct and indirect effects on insect
405 population dynamics. *Ecology Letters*, **15(5)**, pp.502-508.
- 406 Boggs, C.L. (2016) The fingerprints of global climate change on insect populations. *Current*
407 *Opinion in Insect Science*, **17**, pp.69-73.
- 408 Bradshaw, W. E. & Holzapfel, C. M. (2010a) Light, time, and the physiology of biotic response to
409 rapid climate change in animals. *Annual review of physiology*, **72**, 147-166.
- 410 Bradshaw, W. E. & Holzapfel, C. M. (2010b) Insects at not so low temperature: Climate change in
411 the temperate zone and its biotic consequences. *Low Temperature Biology of Insects*, Cambridge
412 University Press, Cambridge, UK, pp. 242-275.
- 413 Breed, G A., Stichter, S. & Crone, E. E. (2013) Climate-driven changes in northeastern US butterfly
414 communities. *Nature Climate Change*, **3**, 142– 45.
- 415 Burnham, K. P. & Anderson, D. R. (2002) Model selection and multimodel inference: a practical
416 information-theoretic approach. 2nd ed. New York, Springer-Verlag.
- 417 CABI, (2022) Invasive Species Compendium. Wallingford, UK: CAB International.
418 www.cabi.org/isc [13. January 2022.]
- 419 C FC Lt. Fraser (1936) The Fauna of British India, including Ceylon and Burma, Odonata Vol. III.
420 Red Lion Court, Fleet Street, London: Taylor and Francis. pp. 414–416.
- 421 Chambers, L. E. (2009) Evidence of climate related shifts in Australian phenology. In Proceedings
422 of 18th World IMACS Congress and MODSIM09 *International Congress on Modelling and*
423 *Simulation*, pp. 13-17.
- 424 Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S.,
425 Ahern, J.R., Bell-Dereske, L.P., Roy, C.L., Meza-Lopez, M. and Carrillo, J., 2012. Does
426 phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis.
427 *Ecology Letters*, **15(6)**, pp.627-636.
- 428 Chapman, J.W. Drake, V.A. & Reynolds DR. (2011) Recent insights from radar studies of insect
429 flight. *Annu Rev Entomol* **56**, 337–56.
- 430 Chapman, J. W., Bell, J. R., Burgin, L. E., Reynolds, D. R., Pettersson, L. B., Hill, J. K. ... &
431 Thomas, J. A. (2012) Seasonal migration to high latitudes results in major reproductive benefits
432 in an insect. *Proceedings of the National Academy of Sciences*, **109(37)**, 14924-14929.
- 433 Chapman, J.W. Reynolds, D.R. & Wilson, K. (2015) Longrange seasonal migration in insects:
434 mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters*, **18**, 287–302.
- 435 Chowdhury, S., Fuller, R. A., Dingle, H., Chapman, J. W. & Zalucki, M. P. (2021). Migration in
436 butterflies: a global overview. *Biological Reviews*, **96(4)**, 1462-1483.
- 437 Conrad, K. F., Woiwod, I. P., Parsons, M., Fox, R., & Warren, M. S. (2004). Long-term population
438 trends in widespread British moths. *Journal of Insect Conservation*, **8(2)**, 119-136.
- 439 Cressman, K. (2013) Climate change and locusts in the WANA Region. *Climate change and food*
440 *security in West Asia and North Africa*. pp. 131-143. Springer, Dordrecht.
- 441 Dingle, H. (1996) *Migration: the biology of life on the move* (Vol. 480). New York: Oxford
442 University Press.
- 443 Dingle, H., Blakley, N. R., & Miller, E. R. (1980). Variation in body size and flight performance in
444 milkweed bugs (*Oncopeltus*). *Evolution*, 371-385.
- 445 Dingle, H. & Drake, V. A. (2007) What is migration?. *Bioscience*, **57(2)**, 113-121.

- 446 Drake, V.A. & Gatehouse, A.G. (1995) *Insect migration: tracking resources through space and time*.
447 Cambridge, UK: Cambridge University Press.
- 448 Dunn, P.O. & Møller, A.P. eds., (2019) *Effects of climate change on birds*. Oxford University Press.
- 449 Farrow, R. A & McDonald, G. (1987). Migration strategies and outbreaks of noctuid pests in
450 Australia. *International Journal of Tropical Insect Science*, **8(4-5-6)**, 531-542.
- 451 Forrest, J. R. (2016) Complex responses of insect phenology to climate change. *Current opinion in*
452 *insect science*, **17**, 49-54.
- 453 Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect*
454 *Conservation and Diversity*, **6(1)**, 5-19.
- 455 Fox, R., Oliver, T. H., Harrower, C., Parsons, M. S., Thomas, C. D., & Roy, D. B. (2014).
456 Long-term changes to the frequency of occurrence of British moths are consistent with opposing
457 and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51(4)**, 949-
458 957.
- 459 GBIF.org (2022) GBIF Home Page. Available from: <https://www.gbif.org>. [13. January 2020.]
- 460 Gallinat, A. S., Primack, R. B. & Wagner, D. L. (2015) Autumn, the neglected season in climate
461 change research. *Trends in Ecology & Evolution*, **30(3)**, 169-176.
- 462 Halsch, C.A., Shapiro, A.M., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P. & Forister,
463 M.L. (2021) Insects and recent climate change. *Proceedings of the national academy of sciences*,
464 **118(2)**.
- 465 Holland, R.A., Wikelski, M. & Wilcove, D.S. (2006) How and why do insects migrate? *Science*,
466 **313**, 794–796.
- 467 Hu, C., Kong, S., Wang, R., Long, T. & Fu, X. (2018) Identification of migratory insects from their
468 physical features using a decision-tree support vector machine and its application to radar
469 entomology. *Scientific Reports*, **8(1)**, pp.1-11.
- 470 Hu, G., Lu, M. H., Reynolds, D. R., Wang, H. K., Chen, X., Liu, W. C. ... & Chapman, J. W. (2019).
471 Long-term seasonal forecasting of a major migrant insect pest: the brown planthopper in the
472 Lower Yangtze River Valley. *Journal of Pest Science*, **92(2)**, 417-428.
- 473 Hu, G., Stefanescu, C., Oliver, T. H., Roy, D. B., Breerton, T., Van Swaay, C., ... & Chapman, J. W.
474 (2021). Environmental drivers of annual population fluctuations in a trans-Saharan insect
475 migrant. *Proceedings of the National Academy of Sciences*, **118(26)**, e2102762118.
- 476 Jauker, F. & Wolters, V. (2008) Hover flies are efficient pollinators of oilseed rape. *Oecologia*, 156,
477 819.
- 478 Juhász, E., Gó, Á., Bali, D., Kerékgyártó, F., Katona, G. & Végvári, Zs. (2021) Long-term temporal
479 patterns in flight activities of a migrant diurnal butterfly. *Insect Science*, **28(3)**, 839-849.
- 480 Jonko, C. (2022) Lepidoptera Mundi. <https://lepidoptera.eu/>, [21. January, 2022.]
- 481 Kennedy, J. S. (1951). The migration of the desert locust (*Schistocerca gregaria* Forsk.). I. The
482 behaviour of swarms. II. A theory of long-range migrations. *Philosophical Transactions of the*
483 *Royal Society of London. Series B, Biological Sciences*, 163-290.
- 484 Lemoine, N. & Böhning-Gaese, K. (2003) Potential impact of global climate change on species
485 richness of long-distance migrants. *Conservation Biology*, **17**, 577–586
- 486 Lemoine, N. P. (2015). Climate change may alter breeding ground distributions of eastern migratory
487 monarchs (*Danaus plexippus*) via range expansion of *Asclepias* host plants. *PLoS one*, **10(2)**,
488 e0118614.
- 489 Lortie, C.J., Aarssen, L.W., Budden, A.E., Koricheva, J.K., Leimu, R. & Tregenza, T. (2007)
490 Publication bias and merit in ecology. *Oikos*, **116(7)**, 1247-1253.
- 491 Luquet, M., Hullé, M., Simon, J. C., Parisey, N., Buchard, C. & Jaloux, B. (2019) Relative
492 importance of long-term changes in climate and land-use on the phenology and abundance of
493 legume crop specialist and generalist aphids. *Insect science*, **26(5)**, 881-896.
- 494 Lydolph, P.E., Temple, D. & Temple, D. (1985) The climate of the earth. *Government Institutes*.
- 495 Mak, M., 2011. *Atmospheric dynamics*. Cambridge University Press.

- 496 Menz, M.H., Scacco, M., Bürki-Spycher, H.M., Williams, H.J., Reynolds, D.R., Chapman, J.W. &
 497 Wikelski, M., 2022. Individual tracking reveals long-distance flight-path control in a nocturnally
 498 migrating moth. *Science*, **377(6607)**, pp.764-768.
- 499 Musolin, D.L. and Saulich, A.K. (2012) Responses of insects to the current climate changes: from
 500 physiology and behavior to range shifts. *Entomological Review*, **92(7)**, pp.715-740.
- 501 Needham, J. G., Westfall Jr. M J, & May, M. L. (2000). Dragonflies of North America (rev. ed.).
 502 Gainesville, FL: Scientific Publishers. pp. 719–720. ISBN 0-945417-94-2.
- 503 Ohba, M., Wasano, N. and Matsuda-Ohba, K. (1999) Considerations on the northern expansion of
 504 the summer migration range in the oleander hawk-moth *Daphnis nerii* (Linnaeus)(Lepidoptera:
 505 Sphingidae). *Applied entomology and zoology*, **34(3)**, 345-349.
- 506 Oberhauser, K. and Townsend Peterson, A. (2003) Modelling current and future potential wintering
 507 distributions of eastern North American monarch butterflies. Proceedings of the *National*
 508 *Academy of Sciences*, **100**, 14063–14068
- 509 Parmesan, C., Burrows, M. T., Duarte, C. M., Poloczanska, E. S., Richardson, A. J., Schoeman, D.
 510 S. and Singer, M. C. (2013) Beyond climate change attribution in conservation and ecological
 511 research. *Ecology letters*, **16**, 58-71.
- 512 R Core Team (2022). R: A language and environment for statistical computing. R Foundation for
 513 Statistical Computing, Vienna, Austria URL <https://www.R-project.org/>
- 514 Rainey, R. C. (1963) Meteorology and the migration of desert locusts. Applications of synoptic
 515 meteorology in locust control. Technical Notes. *World Meteorological Organization.*, 54.
- 516 Rankin, M. A. & Burchsted, J. C. A. (1992). The cost of migration in insects. *Annual review of*
 517 *entomology*, **37(1)**, 533-559.
- 518 Robinet, C. & Roques, A. (2010) Direct impacts of recent climate warming on insect populations.
 519 *Integrative zoology*, **5(2)**, 132-142.
- 520 Robinson, R. A., Learmonth, J. A., Hutson, A. M., Macleod, C. D., Sparks, T. H., Leech, D. I. ... and
 521 Crick, H. Q. (2005) Climate change and migratory species. The Nunnery, Thetford, Norfolk:
 522 *British Trust for Ornithology*. p.414
- 523 Satterfield, D. A., Sillett, T. S., Chapman, J. W., Altizer, S. and Marra, P. P. (2020) Seasonal insect
 524 migrations: massive, influential, and overlooked. *Frontiers in Ecology and the Environment*,
 525 **18(6)**, 335-344.
- 526 Schaefer, G. W. (1969) Radar studies of locust, moth and butterfly migration in the Sahara.
 527 *Proceedings of the Royal Entomological Society London C*, **34(33)**, 39-40.
- 528 Sihag, R. C. (2014) Phenology of migration and decline in colony numbers and crop hosts of giant
 529 honeybee (*Apis dorsata* F.) in semiarid environment of Northwest India. *Journal of Insects*,
 530 2014.
- 531 Sorensen, W.C. (1995) *Brethren of the net: American entomology*, Tuscaloosa, Alabama: University
 532 of Alabama Press. pp. 1840–1880.
- 533 Sparks, T. H., Roy, D. B. and Dennis, R. L. H. (2005) The influence of temperature on migration of
 534 Lepidoptera into Britain. *Global Change Biology*, **11(3)**, 507-514.
- 535 Stefanescu, C., Alarcón, M. & Ávila, A. (2007). Migration of the painted lady butterfly, *Vanessa*
 536 *cardui*, to north-eastern Spain is aided by African wind currents. *Journal of Animal Ecology*,
 537 888-898.
- 538 Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T., ... & Chapman, J. W.
 539 (2013). Multi-generational long-distance migration of insects: studying the painted lady butterfly
 540 in the Western Palaearctic. *Ecography*, **36(4)**, 474-486.
- 541 Tenhumberg, B. and Poehling, H.M. (1995) Syrphids as natural enemies of cereal aphids in
 542 Germany: aspects of their biology and efficacy in different years and regions. *Agriculture*,
 543 *Ecossystems & Environment*, **52**, 39–43.
- 544 Torniaainen, J. & Mikonranta, L. (2018). The origins of northern European *Autographa gamma*
 545 individuals evaluated using hydrogen stable isotopes. *Ecological Entomology*, **43(5)**, 699-702.

- 546 Urquhart, F. A. and Urquhart, N. R. (1978) Autumnal migration routes of the eastern population of
547 the monarch butterfly (*Danaus p. plexippus* L.; Danaidae; Lepidoptera) in North America to the
548 overwintering site in the Neovolcanic Plateau of Mexico. *Canadian Journal of Zoology*, **56(8)**,
549 1759-1764.
- 550 Végvári, Z., Juhász, E., Tóth, J. P., Barta, Z., Boldogh, S., Szabó, S., and Varga, Z. (2015).
551 Life-history traits and climatic responsiveness in noctuid moths. *Oikos*, **124(2)**, 235-242.
- 552 Westbrook, J., Fleischer, S., Jairam, S., Meagher, R. and Nagoshi, R. (2019) Multigenerational
553 migration of fall armyworm, a pest insect. *Ecosphere*, **10(11)**, e02919.
- 554 Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E. ... and
555 Ault, T. R. (2012) Warming experiments underpredict plant phenological responses to climate
556 change. *Nature*, **485(7399)**, 494-497.
- 557 Wotton, K. R., Gao, B., Menz, M. H., Morris, R. K., Ball, S. G, Lim, K. S., ... & Chapman, J. W.
558 (2019). Mass seasonal migrations of hoverflies provide extensive pollination and crop protection
559 services. *Current Biology*, **29(13)**, 2167-2173.
- 560 Woodward, G.U.Y., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., Cross,
561 W.F., Friberg, N., Ings, T.C., Jacob, U. & Jennings, S. (2010) Ecological networks in a changing
562 climate. In *Advances in ecological research* (Vol. 42, pp. 71-138). Academic Press.
563

564 **Tables**

565

566 **Table 1.** Model selection table for the GLMM fitted on the climatic effect as response variable.567 Significant relationships are marked in bold. β indicates parameter estimates, SEu stands for

568 unconditional SE-s.

569

570

Predictor	β	SEu	Adjusted SE	z-value	p-value
Intercept	-39.2720	27.4529	24.4634	1.497	0.1455
Climate zone					
(temperate/cold)	-29.6213	15.7100	16.0134	1.7235	0.0421
Climate zone					
(tropical/temperate)	-1.4781	12.2672	12.1112	0.1217	0.9761
Climate zone					
(tropical/temperate/cold)	11.1502	14.8287	15.1793	0.7851	0.4601
log(body size)	14.1672	6.6834	6.7955	2.0677	0.0305
Wintering stage (egg)	0.1336	3.3176	3.2301	0.0448	0.9691
Wintering stage (larva)	-0.0256	7.6678	7.7841	0.0029	0.9931
Wintering stage					
(larva/pupa/adult)	-6.6743	3.3613	3.2822	0.0001	0.9998
Wintering stage (pupa)	-0.0232	1.4861	1.4111	0.0256	0.9756

571

572

573

574 **Table 2.** Model selection table for the GLMM fitted on the climatic complexity as response575 variable. Significant relationships are marked in bold. β indicates parameter estimates, SEu stands

576 for unconditional SE-s.

577

578

Predictor	β	SEu	Adjusted SE	z-value	p-value
Intercept	10.2153	12.7420	12.6874	0.891	0.4175
Climate zone					
(temperate/cold)	-15.3392	13.5591	13.7842	1.2347	0.2732
Climate zone					
(tropical/temperate)	-15.5187	9.831	9.864	1.5662	0.1325
Climate zone					
(tropical/temperate/cold)	-37.2249	14.7878	15.2844	2.4751	0.1120
log(body size)	8.9562	2.4462	2.4507	3.6951	0.0027
Wintering stage (egg)	33.1471	41.2448	41.8629	0.7875	0.4342
Wintering stage (larva)	15.6261	1.4340	1.5763	0.0001	0.9887
Wintering stage					
(larva/pupa/adult)	8.0409	43.8961	44.6505	0.1802	0.9101
Wintering stage (pupa)	18.0587	32.9112	33.107	0.5683	0.6221

579

580

581

582

583

584

585

586 **Table 3.** Model selection table for the GLMM fitted on the climatic scale as response variable. β
 587 indicates parameter estimates, SEu stands for unconditional SE-s.
 588
 589

Predictor	β	SEu	Adjusted SE	z-value	p-value
	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	10.8613	4.9566	4.8230	2.1527	0.0314
log(body size)	0.0877	1.1285	1.1621	0.0729	0.9667
Climate zone (temperate/cold)	-0.0083	2.0566	2.0691	0.0047	0.9982
Climate zone (tropical/temperate)	0.0066	1.5563	1.6814	0.0078	0.9989
Climate zone (tropical/temperate/cold)	-0.0072	2.1134	2.0991	0.0019	0.9913
Wintering stage (egg)	0.1193	4.4555	4.6856	0.0433	0.9765
Wintering stage (larva)	24.1314	3.3791	3.4356	0.0002	0.9989
Wintering stage (larva/pupa/adult)	3.8483	5.7302	5.8495	0.0000	0.9991
wintering.stagepupa	0.0378	5.1617	5.1991	0.0074	0.9977

590
 591
 592
 593
 594
 595
 596
 597
 598
 599

600 **Figure legends**

601

602 **Fig. 1. a)** Taxonomic distribution of migratory insects, indicating the number of species classified
603 into insect orders; **b)** Climatic zonal distribution of migratory insects, indicating the number of
604 species occurring in major climatic zones; **c)** Spatial distribution of migratory insects, indicating the
605 number of species occupying various continents.

606

607

608 Fig 2. Relationship between climatic effect (direct or indirect) and climate zone (defined as the
609 major climatic zones intersecting the distribution range) for migratory insects.

610

611 Fig 3. Relationship between climatic effect and log-transformed body size for migratory insects,
612 showing the level of significance for the GLMM fitted on the climatic effect as a function of body
613 size.

614 **Figures**

615

616 Fig 1.

617

618

619

620

621

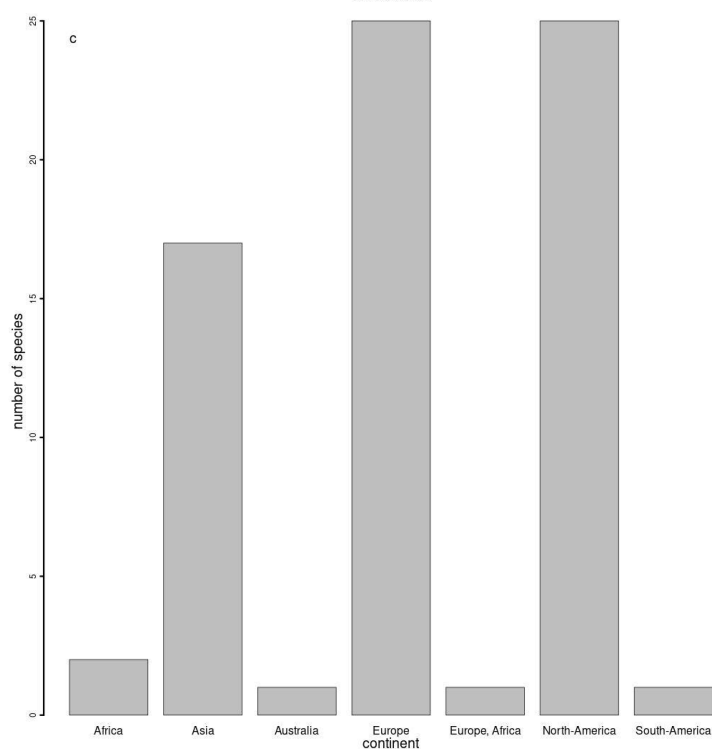
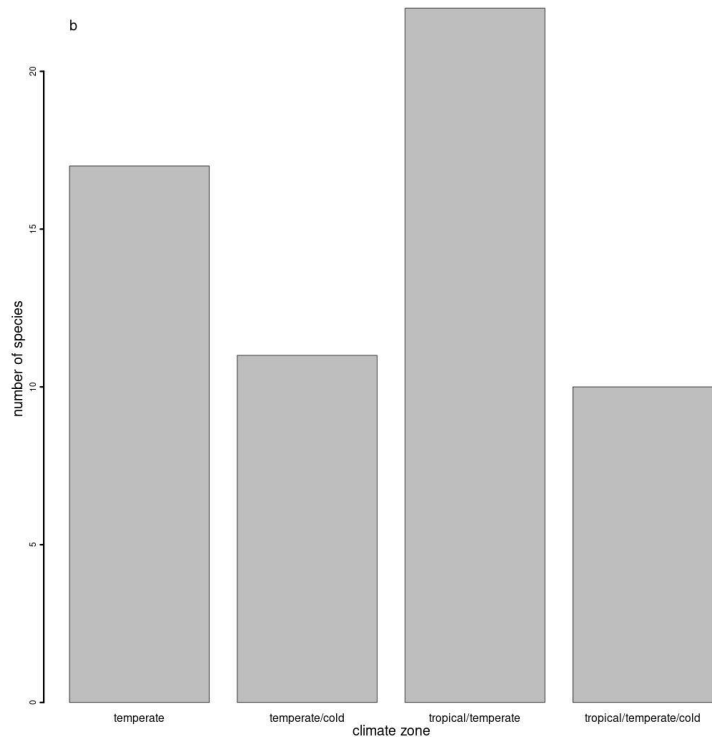
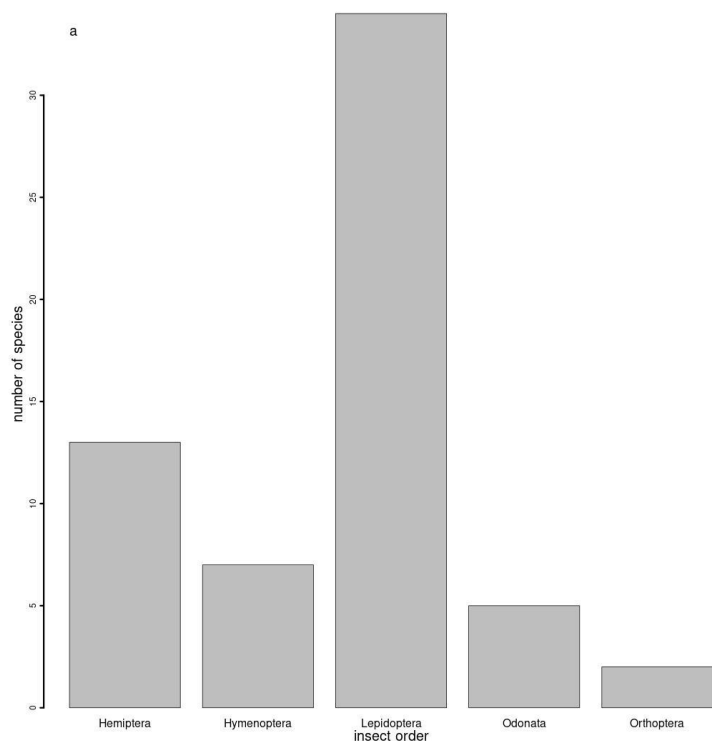
622

623

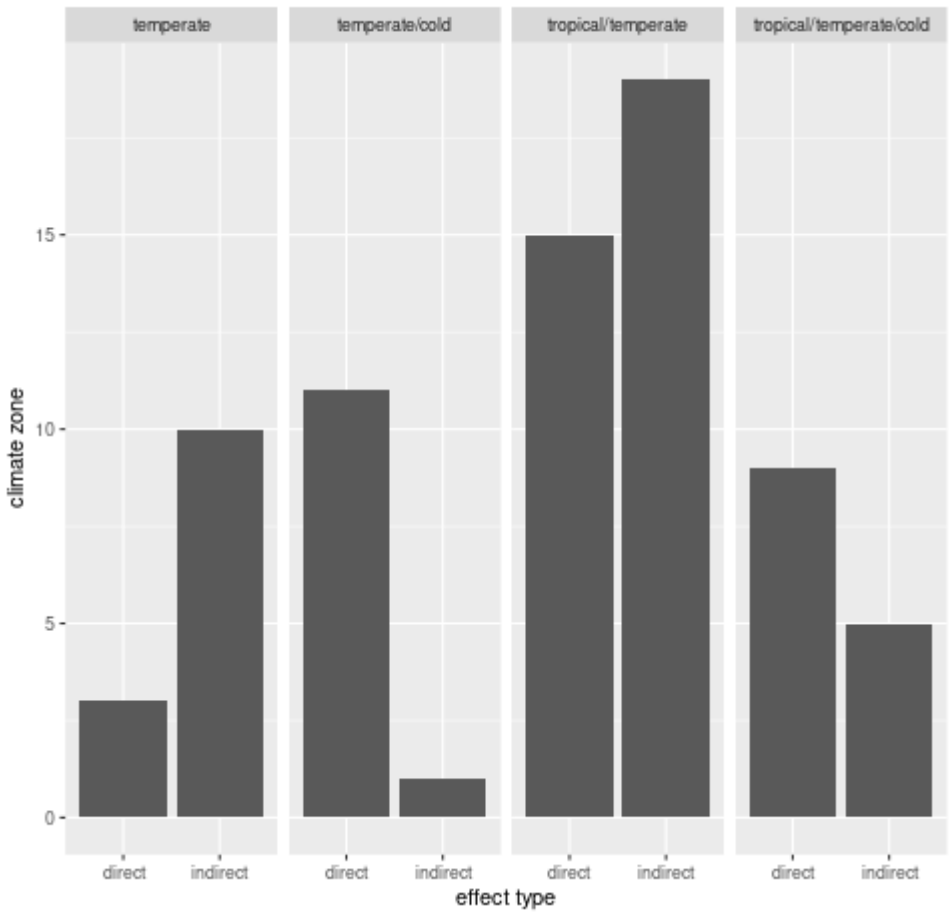
624

625

626



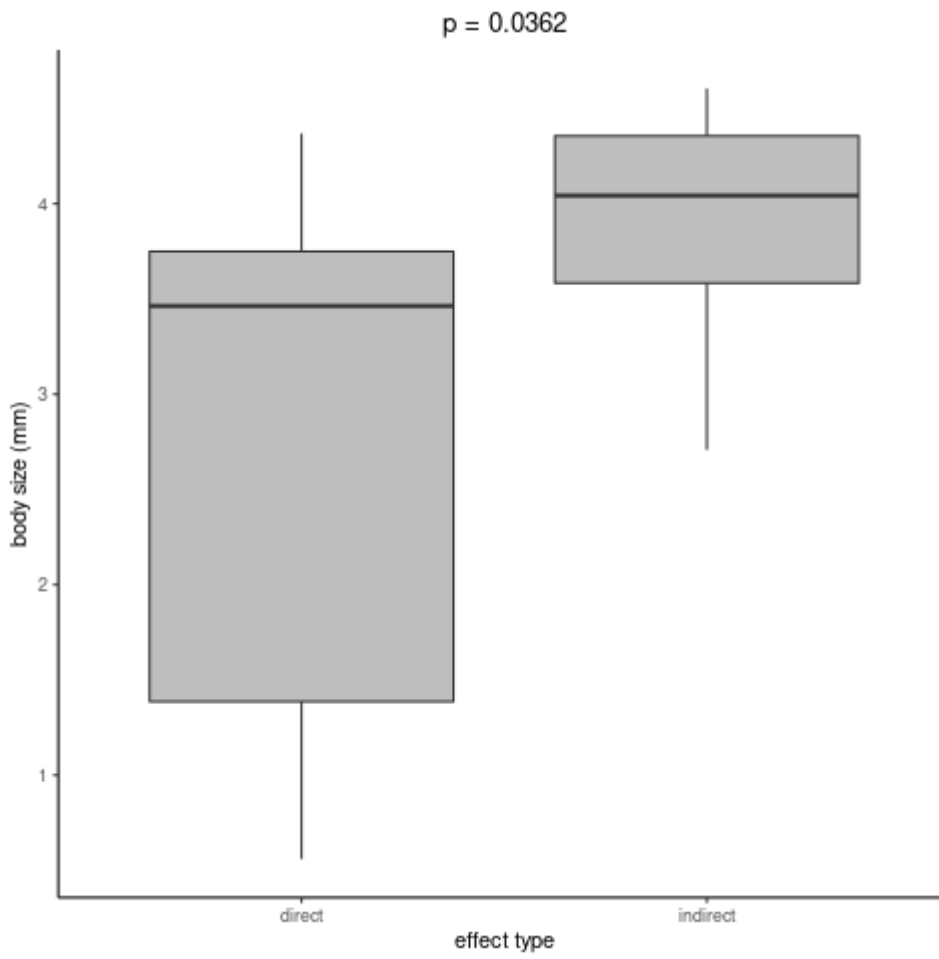
627
628 Fig 2.
629



630
631
632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651

652
653
654
655
656

657 Fig 3.
658



659
660
661
662