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1 **Impacts of climate change on high priority fruit fly species in Australia**

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11 **Abstract**

12 Tephritid fruit flies are among the most destructive horticultural pests and pose risks to
13 Australia's multi-billion-dollar horticulture industry. Currently, there are 11 pest fruit fly
14 species of economic concern present in various regions of Australia. Of these, nine are native
15 to this continent (*Bactrocera aquilonis*, *B. bryoniae*, *B. halfordiae*, *B. jarvisi*, *B. kraussi*, *B.*
16 *musae*, *B. neohumeralis*, *B. tryoni* and *Zeugodacus cucumis*), while *B. frauenfeldi* and *Ceratitis*
17 *capitata* are introduced. To varying degrees these species are costly to Australia's horticulture
18 through in-farm management, monitoring to demonstrate pest freedom, quarantine and trade
19 restrictions, and crop losses. Here, we used a common species distribution modelling approach,
20 Maxent, to assess habitat suitability for these 11 species under current and future climate
21 scenarios. These projections indicate that the Wet Tropics is likely to be vulnerable to all 11
22 species. The east coast of Australia will likely remain vulnerable to multiple species until at
23 least 2070. Both the Cape York Peninsula and Northern Territory are also likely to be
24 vulnerable, however, extrapolation to novel climates in these areas decrease confidence in
25 model projections. The climate suitability of current major horticulture regions in north-

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26 western Australia, the Northern Territory, southern-central regions of New South Wales and
27 southern Victoria to these pests is projected to increase as climate changes. Our study highlights
28 areas at risk of pest range expansion in the future, to guide Australia's horticulture industry in
29 developing effective monitoring and management strategies.

30

31 **Keywords:** Tephritidae, fruit flies, species distribution modelling, habitat suitability, climate
32 change

33

34 Introduction

35 Tephritid fruit flies are one of the most destructive and economically significant pest insect
36 families, attacking a wide range of fruit and vegetables. While the family contains more than
37 4000 species, around 350 are recognized as economically important horticultural pests [1] that
38 have significant impacts on global horticultural production and market access. In Australia, the
39 average annual value of crops susceptible to fruit flies is ~\$4.8 billion [1], and the National
40 Fruit Fly Strategy has identified 46 species as 'high priority pests' [2] of concern. The majority
41 of these species are exotic to Australia, primarily found in South-East Asia and the South
42 Pacific [1, 2], and are yet to establish populations in Australia. Of the 11 species that are
43 currently present in Australia [1-3] (Table 1), seven are reported to cause significant economic
44 losses (*Bactrocera aquilonis*, *B. jarvisi*, *B. neohumeralis*, *B. musae*, *B. tryoni*, *Ceratitis*
45 *capitata*, and *Zeugodacus cucumis*) [1, 4]. Combined, these species infest a wide variety of
46 hosts, with some (e.g. *B. frauenfeldi*, *B. jarvisi*, *B. neohumeralis*, *B. tryoni* and *Ceratitis*
47 *capitata*) [3] being highly polyphagous.

48

49 The distributions of Australia's pest fruit fly species are influenced by their climatic tolerances
50 and the distributions of their hosts. *Bactrocera* originated in tropical regions, and have their

51 highest richness in rainforests [5]. However, over the last 100 years, as horticulture has
52 proliferated across Australia, some species have expanded their geographic range and host
53 breadth [6]. Of the 11 high priority fruit fly species presently on the continent, three are
54 currently restricted to north-east Queensland (*B. frauenfeldi*, *B. kraussi* and *B. musae*) [7]. In
55 contrast, the geographic range of *B. neohumeralis* (Lesser Queensland fruit fly) extends along
56 eastern Australia, from Queensland to central New South Wales (NSW) [3, 4, 7]. Previous
57 climatic analysis indicates that this species also has the potential to establish elsewhere in
58 northern Australia [4]. The remaining species have substantially wider climate tolerances, and
59 are found across broad regions of the continent. For instance, *B. tryoni* (Qfly) ranges across
60 much of eastern Australia, eastern Queensland and northern regions of the Northern Territory
61 [8]. *Bactrocera jarvisi* (Jarvis' fruit fly) extends from northwest Western Australia, across the
62 Northern Territory to northern Queensland and the Torres Strait Islands [4, 9], and, in
63 favourable years, may spread down the east coast of Australia into northern coastal NSW [4,
64 9]. Hence, *B. jarvisi* and *B. tryoni* have overlapping geographic ranges and infest many of the
65 same hosts [4]. *Ceratitis capitata* (Medfly) originated from the Afrotropical region [10], and
66 was introduced into the Perth area (Western Australia) in the late 1800s [4]. Before quarantine
67 controls were developed, this species spread to NSW, Victoria, and other parts of Australia
68 [11]. However, for reasons that remain unclear, Qfly is believed to have displaced Medfly
69 throughout most of its former Australian range [12], and now Medfly is confined to Western
70 Australia, with occasional detections in South Australia [13].

71

72 Under current climate conditions, most of these 11 fruit fly species pose threats to Australia's
73 horticulture industries, as well as to backyard growers. As such, controlling fruit flies is
74 imperative for the viability of Australian horticulture, necessitating in-farm management and
75 pest treatment, monitoring to demonstrate pest freedom, and quarantine and trade restrictions

76 [1, 2]. These controls, along with loss of market access, are estimated to cost Australian
77 growers \$100 million per annum [4], in addition to losses of up to \$159 million per annum due
78 to infestation of fruit and vegetable crops [14].

79

80 For those areas where fruit flies are found, the annual cost, as reported in 2012, of bait and
81 cover spray, as well as post-harvest treatments, amount to \$269 ha⁻¹ and \$62.36 tonne⁻¹,
82 respectively [15], while maintaining fruit fly free areas is estimated to exceed \$28 million per
83 annum based on data from 2009-2011 [16]. However, restrictions were recently placed on the
84 use of insecticides to control fruit flies due to concerns about toxicity [17], with dimethoate
85 and fenthion suspended or highly restricted for many horticultural crops [17-20]. Other
86 approaches, including Sterile Insect Techniques, are now being explored. Regardless, it has
87 been estimated that the annual likelihood of an incursion by an exotic fruit fly species is 21%
88 [15], and the annual cost of eradicating these incursions is ~\$13 million [16], with rapid
89 responses to outbreaks being crucial for eradication [21]. Even brief incursions can result in
90 significant economic damage due to market access restrictions that may be imposed. However,
91 climate change is likely to alter the distribution of suitable habitat for fruit fly species and areas
92 vulnerable to outbreaks, and this could have serious repercussions for Australian horticulture
93 [22].

94

95 Previous studies [22-24] have used the semi-mechanistic species distribution model (SDM),
96 CLIMEX, to estimate the potential geographic distributions of several high priority fruit fly
97 species, based on their performance along climatic gradients. While highly useful in furthering
98 our understanding of climate impacts on fruit flies, these studies have either focused on other
99 countries [24-26] or have explored global patterns of the distribution of suitable climate [22,
100 23]. Here we assess how climate change may result in shifts to the distribution of suitable

101 habitat for the 11 high priority fruit fly species present in Australia, using the correlative SDM,
 102 Maxent [27]. This SDM has been used extensively to assess the distribution of suitable habitat
 103 for a broad range of pests and invasive species [26, 28-31]. We also highlight areas at risk of
 104 pest range expansion, to guide Australia's horticulture industries in development of effective
 105 monitoring and management strategies.

106

107 **Table 1. Eleven economically-significant tephritid pest species present in Australia.**

Species	Common name	Geographical Range	Major Commercial Hosts [32]	References
<i>Bactrocera aquilonis</i> (May)	Northern Territory fruit fly	Top End of the Northern Territory (NT), northern areas of Western Australia	Bell pepper, tomato, lemon, mandarin, grapefruit, apple, mango, peach	1
<i>Bactrocera bryoniae</i> (Tryon)	N/A	Torres Strait Islands, mainland Queensland, northern Western Australia, NT, NSW as far south as Sydney	Chilli, tomato	3
<i>Bactrocera halfordiae</i> (Tryon)	Halfordia fruit fly	North Queensland south to the Sydney region in NSW	Citrus	3
<i>Bactrocera jarvisi</i> (Tryon)	Jarvis' fruit fly	North-western Western Australia, NT, north-west Queensland, eastern Australia from Cape York to Sydney, NSW	Mango, peach, banana, pear, apple, pawpaw, persimmon	3
<i>Bactrocera kraussi</i> (Hardy)	Krauss' fruit fly	Torres Strait Islands, northeast Queensland as far south as Townsville	Grapefruit, mandarin, orange, mango, peach and banana	3, 7
<i>Bactrocera musae</i> (Tryon)	Banana fruit fly	Torres Strait Islands, northeast Queensland as far south as Townsville	Banana	3, 7
<i>Bactrocera neohumeralis</i> (Tryon)	Lesser Queensland fruit fly	Torres Strait Islands, eastern Queensland, northern NSW	Mango, papaw, persimmon, avocado, banana, passionfruit, apple, apricot, plum, peach,	3

			citrus, capsicum, chilli, tomato	
<i>Bactrocera tryoni</i> (Froggatt)	Queensland fruit fly (Qfly)	Central and Top End of NT, eastern Australia, Victoria	Mango, papaw, avocado, grapefruit, passionfruit, strawberry, peach, pear, apple, banana, persimmon, chilli, capsicum, tomato, eggplant	3,31
<i>Zeugodacus cucumis</i> (French) (formerly <i>Bactrocera cucumis</i>)	Cucumber fruit fly	Eastern Queensland, north-eastern NSW, NT	Cucumber, pumpkin, zucchini, squash, passionfruit, tomato, pawpaw	3
<i>Bactrocera frauenfeldi</i> (Schiner)	Mango fruit fly	Native to Papua New Guinea and surrounding islands, spread to Torres Strait Islands and northern Queensland as far south as Townsville	Mango, banana, passionfruit, citrus, chilli	7
<i>Ceratitis capitata</i> (Wiedemann)	Mediterranean fruit fly (Medfly)	Native to Africa, spread to the Mediterranean regions, Western Australia, occasional detections in South Australia and NT are eradicated.	Mango, papaw, apple, peach, pear, citrus	3, 28, 31

108 Table 1. Eleven tephritid pest species present in Australia, including nine natives (*B. aquilonis*, *B. bryoniae*, *B.*
109 *halfordiae*, *B. jarvisi*, *B. kraussi*, *B. musae*, *B. neohumeralis*, *B. tryoni* and *Z. cucumis*) and two introduced species
110 (*B. frauenfeldi* and *C. capitata*), and their major commercial hosts.

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112

113 Methodology

114 Species occurrence data

115 We collected occurrence data for the 11 species from five main sources: the Australian Plant
116 Pest Database (APPD; [http://www.planthealthaustralia.com.au/resources/australian-plant-](http://www.planthealthaustralia.com.au/resources/australian-plant-pest-database)
117 [pest-database](http://www.planthealthaustralia.com.au/resources/australian-plant-pest-database), accessed 15th March 2017), the Atlas of Living Australia (ALA;
118 <http://www.ala.org.au>, 22nd December, 2016), the Global Biodiversity Information Facility

119 (GBIF, <https://www.gbif.org>, 28th June, 2017), trap data, and existing literature. APPD is a
120 national digital database of plant pest and pathogen specimens held within herbaria and insect
121 collections across Australia. It is a powerful tool for market access and emergency responses
122 to pest incursion, and supports associated research activities. ALA is Australia's largest digital
123 database of species occurrence records, containing information from a wide array of data
124 providers including Australia's major museums and government departments. GBIF provides
125 similar data at a global scale. Before downloading data from APPD, ALA and GBIF, we
126 applied filters to restrict records to those that were resolved to species-level, were dated no
127 earlier than 1 January 1950, contained valid geographic coordinates, and were not flagged as
128 'environmental outliers'.

129

130 We also collected trap data from various state government departments (Biosecurity and Food
131 Safety, Department of Primary Industries, NSW; Biosecurity Queensland and the Queensland
132 Department of Agriculture and Fisheries; Department of Economic Development, Jobs,
133 Transport and Resources, Victoria; and Department of Primary Industries and Regions South
134 Australia (PIRSA)). Trap data from these sources were collected at different periods from 1996
135 to 2017. Finally, we also obtained occurrence data from the literature [1-4, 6, 7, 11, 33-37].

136

137 **Major commercial fruit and vegetable hosts**

138 For each of the 11 fruit fly species, we compiled information on the major commercial hosts
139 on which infestation has been recorded. For this purpose, we defined major fruit and vegetable
140 host species according to the Australian Horticulture Statistics Handbook (HSHB;
141 www.horticulture.com.au) for the year 2016/2017 [32]. This document consolidates
142 horticulture statistics of interest to industry members and other stakeholders. The data
143 contained in HSHB were derived from the Australian Bureau of Statistics, projects funded by

144 Hort Innovation, international trade sources and horticulture industry representative bodies
145 where available.

146

147 **Climate data**

148 For current and future climate conditions we used the bioclimatic variables available within
149 the WorldClim database, at a spatial resolution of 30 arc-seconds [38] (approximately 1 km;
150 <http://www.worldclim.org>). These data, based on meteorological records for the period 1960–
151 1990, comprise 19 climatic variables, 11 of which are temperature-based while eight relate to
152 precipitation. Combined, the data represent annual trends, seasonality, and limiting or extreme
153 environmental conditions. Assuming that host plants are available, temperature and moisture
154 are the key factors influencing fruit fly reproduction and survival [18, 39]. Thus, these variables
155 were chosen as predictor candidates based on the fruit flies' biology and ecological
156 requirements, and similar habitat suitability studies undertaken on other insects [40]. For each
157 species, we identified a set of ecologically-relevant variables, with minimal collinearity, that
158 resulted in high predictive power for the model [41] (described below).

159

160 When projecting the future suitability of habitat, we considered a range of climate scenarios to
161 acknowledge this important aspect of uncertainty. We choose six global climate models
162 (GCMs) recommended by CSIRO as being useful for Australian climate impact assessments
163 [42], and for which data were available at our chosen spatial resolution for the Representative
164 Concentration Pathway 8.5 (RCP8.5) [43]. These GCMs included: CanESM2 (The Second
165 Generation of Canadian Earth System Model); ACCESS1.0 (The Australian Community
166 Climate and Earth System Simulator); MIROC5 (Model for Interdisciplinary Research on
167 Climate); HadGEM2-CC (Hadley Centre Global Environmental Model Version 2 Carbon
168 Cycle); NorESM1-M (The Norwegian Earth System Model-Part-1); and GFDL-ESM2M

169 (Global Coupled Climate Carbon Earth System Model Part-1). The CanESM2 model projects
170 a hot future with drying across central regions and higher precipitation in the north-east. The
171 ACCESS1.0 model projects a hot and dry future across most areas of Australia, while MIROC5
172 projects moderate warming, with drying in the north-east and south-west but higher
173 precipitation in central Australia. NorESM1-M projects moderate warming. HadGEM2-CC
174 and GFDL-ESM2M project a hot future with warming typically in central regions. We
175 downloaded the 19 bioclimatic variables from these six models for 20-year periods centred on
176 2030, 2050 and 2070 (<http://www.climatechangeinaustralia.gov.au>). These data were then
177 reprojected to a spatial resolution of 1×1 km (Australian Albers Equal Area, EPSG: 3577) via
178 bilinear interpolation, using the `gdalwarp` function provided by the R package `gdalUtils` [44] in
179 R version 3.3.3 [45].

180

181 **Species Distribution Models**

182 We used the machine learning approach, Maxent (v3.3.3k [27]), to assess habitat suitability for
183 species under current and future climate scenarios. Maxent accommodates presence-only data
184 and has performed well in multimodel assessments [46]. It produces a continuous probability
185 surface, which can be interpreted as an index of habitat suitability given the predictor variables
186 included in model calibration. Detailed descriptions of Maxent are given elsewhere [47, 48].
187 We optimized models by assessing the effects of different combinations of feature types, of
188 competing predictor sets deemed ecologically sensible *a priori*, and of the extent of
189 regularization on model performance. We found that Maxent performed best when product
190 (first-order interactions), linear and quadratic features were used, with a regularization
191 multiplier of 1 (the default), and used this configuration to calibrate our final models.

192

193 Maxent requires background data, to which it compares the environmental characteristics of

194 presence locations. There is flexibility for users to specify which points to use as background,
195 as well as the number of records and the spatial extent from which they are chosen [47].
196 Following Ihlow *et al* [49], we manually generated background points by randomly selecting
197 100,000 cells from terrestrial areas within 200 km of occurrence records of the target species.
198 Our choice of background achieves a balance between fine-scale discrimination of suitable and
199 unsuitable sites along environmental gradients, and generalization of model predictions.

200

201 To assess model performance, we used five-fold cross-validation to reduce model errors that
202 may occur from the random splitting of data into test and training subsets. The performance of
203 each model was evaluated using the area under the receiver operating characteristic curve
204 (AUC), which describes the consistency with which a model ranks randomly chosen presence
205 sites as more suitable than randomly chosen background sites. AUC ranges from 0 to 1, with a
206 value of 0.50 indicating discrimination ability no better than random, while values greater than
207 0.75 indicates that the model has a discriminative ability that is better than “fair” [50]. Cross-
208 validated AUC scores were presumed to reflect the performance of a single final model for
209 each species, which used all available data.

210

211 Following previous studies of pest species [26], continuous habitat suitability scores projected
212 by Maxent models were converted to binary layers (0 = unsuitable, 1 = suitable) using the 10th
213 percentile training presence threshold (i.e. the value that corresponds to 10% training
214 omission). We note that the selection of a threshold value is subjective and may vary depending
215 upon the goals of the study [51], thus we also provide continuous output for current climate as
216 supplemental data (**S1-11 Figs**). For each species, the six binary suitability grids (i.e., one for
217 each GCM, with cells assigned 0 when unsuitable and 1 when suitable) for each time period
218 were summed to produce a consensus map, identifying agreement about the suitability of grid

219 cells across the six climate scenarios. Each species' consensus map was then converting to a
220 binary map indicating whether cells were projected to be suitable under the majority of GCMs
221 (i.e., suitable in < 4 GCMs = 0, suitable in 4 or more = 1). The resulting binary maps were
222 summed across species to identify hotspots - grid cells suitable for multiple pest species.
223 Finally, we compared the distribution of hotspots to that of major horticultural crops.

224

225 When projecting models, extrapolation to conditions beyond the range of the training data may
226 be unreliable. Following Elith *et al.* [52] we developed MESS (multivariate environmental
227 similarity surface) maps to identify regions of extrapolation [52]. By revealing areas with novel
228 environmental conditions, MESS maps can be used as a projection mask, highlighting regions
229 for which projections are unreliable, or as a quantitative measure of prediction uncertainty [52].
230 To assess how novel environments may alter projections of habitat suitability, for each species
231 we visually compared maps of habitat suitability that included projections made in areas with
232 novel environmental conditions to maps that classified these areas as unsuitable.

233

234 All modelling and post-modelling analyses and calculation of statistics were performed in R
235 version 3.1.2 [53]. We used the *sp* [54] and *raster* [55] packages for preparation and
236 manipulation of spatial data, the *dismo* package to fit Maxent models, and custom R code for
237 rapid projection of fitted models.

238

239

240 Results

241 Model Performance

242 Model performance for all species was better than random, with average cross-validated

243 AUC ranging from 0.815 (SD = 0.05; *B. frauenfeldi*) to 0.907 (SD = 0.02; *B. neohumeralis*)

244 **(S1 Table).**

245

246 ***Bactrocera aquilonis***: Our model suggested that suitable habitat for *B. aquilonis* currently
247 exists in the northern regions of the Northern Territory and Western Australia, as well as in
248 northern Queensland, where this fly has not been reported (**S1A-1B Figs**). The variables with
249 the highest permutation importance were precipitation of the wettest quarter (68.9%) and
250 annual mean temperature (28.9%) (**S1 Table**).

251

252 As the century progresses, the geographic extent of suitable habitat for this species is projected
253 to increase and shift southwards under all six scenarios (**S1C-1E Figs**). Further, most areas
254 currently suitable are projected to remain so until at least 2070. By 2030, 21.5% of Australia
255 (i.e. ~1,600,100 km²) is projected to be climatically suitable under at least one climate scenario
256 (**S3 Table**), and this is projected to increase to 39.9% (~3,000,100 km²) by 2070 (**S3 Table**).
257 However, a substantially smaller area is projected suitable under all six scenarios (2030 = 9.2%,
258 ~700,100 km²; 2070 = 20.7%, ~1,590,800 km²) (**S3 Table**). This includes northern Western
259 Australia, much of the Northern Territory, and north-western Queensland (**S1C-1E Figs**).

260

261 Key horticultural crops for *B. aquilonis* are *Mangifera indica* (mango), *Citrus × paradisi*
262 (grapefruit), *Malus domestica* (apple), *Prunus persica* (peach) and *Citrus sp.* (citrus) (**S4**
263 **Table**). The major regions where these crops are currently grown include the Northern
264 Territory and north-east Western Australia. These regions will likely remain suitable for *B.*
265 *aquilonis* until at least 2070. Similarly, fruit growing regions in the Wet Tropics (north-east
266 Queensland) are likely to increase in suitability in the future. Other major host-plant growing
267 regions in the south and east of the continent will likely remain unsuitable (**S1 Fig**).

268

269 ***Bactrocera bryoniae***: Current suitable habitat for *B. bryoniae* is projected to occur along the
270 northern and eastern coastlines (**S2A-2B Figs**). Temperature annual range and precipitation of
271 the driest month contributed the most to the model for this species (42.2% and 27.4%,
272 respectively) (**S1 Table**).

273

274 By 2070, suitable habitat is projected to increase under all scenarios except GFDL-ESM2M
275 (which projects a hot, very dry future) (**S2C-2E Figs; S2 Table**), expanding to the southern
276 coastlines of Victoria and Western Australia. By 2030, 13.5% of Australia (i.e. ~1,038,000
277 km²) is projected to be suitable for *B. bryoniae* under at least one of the climate scenarios,
278 increasing to 20.6% (~1,500,700 km²) by 2070 (**S3 Table**). Under 1-3 scenarios, suitable
279 habitat is projected to shift inland in Queensland and NSW. However, the amount of habitat
280 projected to remain suitable under all six scenarios remains relatively stable from 2030-2070
281 (i.e. spanning 6.5–7.1% of the continent) (**S3 Table**).

282

283 The major horticultural host for *B. bryoniae* is *Capsicum annuum* (chilli) (**S4 Table**). Our
284 model indicates that key growing regions for this crop in Queensland currently contain suitable
285 habitat for *B. bryoniae*, and this will continue to be the case until at least 2070 (**S2 Fig**).

286

287 ***Bactrocera frauenfeldi***: Currently, suitable habitat for this species is projected to be mostly
288 confined to Cape York Peninsula and the Wet Tropics, although there are also small areas in
289 northern Western Australia and the Northern Territory that are classified as suitable, but from
290 which the species has not been recorded (**S3A-3B Figs**). The most important variable in the
291 model for *B. frauenfeldi* was precipitation of the wettest quarter (75.4%) (**S1 Table**).

292

293 As the century progresses, suitable habitat is projected to increase under all scenarios except

294 CanESM2 (**S2 Table**). This scenario projects a hot, very dry future, leading to loss of suitable
295 habitat in northern Queensland by 2050. In contrast, under the ACCESS1.0 scenario (a hot, dry
296 scenario) total range size may increase by 43.6% by 2030. However, by 2070, the Cape York
297 Peninsula region is projected to become unsuitable (**S2 Table**). Overall, 3.3% of Australia (i.e.
298 ~250,400 km²) is projected to be suitable for *B. frauenfeldi* under at least one scenario by 2030,
299 increasingly slightly to 4% (~300,000 km²) by 2070 (**S3 Table**). Only 1.3% (~100,000 km²) of
300 the continent is projected to be suitable under all six scenarios by 2070 (**S3 Table**).

301

302 The major crops for *B. frauenfeldi* are *Mangifera indica* (mango) and *Carcica papaya*
303 (pawpaw) (**S4 Table**). Major production regions in north-western Northern Territory may
304 remain suitable for this species until at least 2070, although there is substantial uncertainty
305 across the climate scenarios. In contrast, it is very likely that the Wet Tropics will remain
306 suitable until at least 2070, irrespective of the climate scenario (**S3 Fig**).

307

308 ***Bactrocera halfordiae***: Suitable habitat for *B. halfordiae* is currently found in the Wet Tropics
309 and subtropics from north Queensland to eastern New South Wales (**S4A-4B Figs**).
310 Precipitation of the driest month (66.8%) and annual mean temperature (32.3%) contributed
311 most to this model (**S1 Table**).

312

313 The geographic extent of suitable habitat is projected to vary considerably across the six
314 climate scenarios, however as the century progresses, gains in new habitat may exceed losses
315 under some scenarios (e.g. see ACCESS and MIROC5 in **S2 Table**). In contrast, under the
316 CanESM2 scenario (which projects a hot future, drying across central regions and higher
317 precipitation in the north-east), total range size may decline by 65.1% by 2030 (**S2 Table**),
318 mostly due to contractions in the south and east, although limited gains in habitat may occur in

319 northern Australia. Similarly, under the HadGEM2 scenario (which projects substantial drying
320 across some regions of the continent), 51.4% of current suitable habitat is projected to be lost
321 by 2030, although by 2070, range expansions may exceed losses (**S2 Table**). By 2030, 6.9%
322 of Australia (i.e. ~500,800 km²) is projected to be suitable for *B. halfordiae* under at least one
323 climate scenario, increasing to 9.9% (~750,900 km²) by 2070 (**S3 Table**).

324

325 Comparing the current and future distribution of suitable habitat for this fly with the major
326 growing regions for its host plants indicates that crops in the Wet Tropics may continue to be
327 at risk, until at least 2070. However, only 1–2 scenarios project horticultural regions in southern
328 Queensland to retain suitable climate (**S4C-4E Figs**). Although horticultural regions along the
329 NSW-Victorian border are currently unsuitable for *B. halfordiae*, some models project these
330 areas to become suitable between 2050–2070 (**S4 Fig**).

331

332 ***Bactrocera jarvisi***: Current suitable habitat for this species is projected to be mostly confined
333 to northern Western Australia, the Top End of the Northern Territory, and eastern Australia
334 from Cape York to NSW (**S5A-5B Figs**). Annual mean temperature (38.0%) and precipitation
335 of driest month (37.2%) had the highest contributions to the model for this species (**S1 Table**).

336 There is substantial consensus across the six scenarios that regions currently suitable for *B.*
337 *jarvisi* will remain so until at least 2070 (**S5C-5E Figs; S2 Table**). In addition, across some
338 models, gains are projected to occur in Western Australia, the Northern Territory and central
339 Queensland. For instance, under the CanESM2 scenario, total range size may increase by
340 45.5% to 58.7% between 2030 and 2070. Similarly, under the hot, very dry scenario projected
341 by ACCESS1.0, 62.5% of future suitable habitat may occur in new areas by 2070 (**S2 Table**).
342 By 2030, 25.8% of Australia (i.e. ~1,980,000 km²) is projected to be suitable for *B. jarvisi* under
343 at least one of the climate scenarios, and due to subsequent gains in suitable habitat, this may

344 increase to 44.3% (~3,390,400 km²) by 2070 (**S3 Table**).

345

346 Comparing the distribution of suitable habitat for this fly with that of its major host crops
347 indicates that crops currently grown in the Top End of the Northern Territory, and in eastern
348 Australia from Cape York to New South Wales, may continue to be at risk until at least 2070.
349 Other major host-plant growing regions in the south and west of the continent will also remain
350 suitable for this species until 2070 (**S5 Fig**).

351

352 ***Bactrocera kraussi***: Suitable habitat for *B. kraussi* is projected to occur across the northern tip
353 of Australia and northeast Queensland, as far south as Townsville (**S6A-6B Figs**). Precipitation
354 of the wettest quarter (75.19%) had the highest contribution to the model of *B. kraussi* (**S1**
355 **Table**).

356

357 The geographic extent of suitable habitat is projected to increase under all six scenarios (**S6C-**
358 **6E Figs; S2 Table**). For example, under the NorESM1-M scenario (a moderate warming
359 scenario with little precipitation change), an area equivalent to 29.6% of current suitable habitat
360 is projected to be gained by 2070 (**S2 Table**). By 2030, 3.1% of Australia (i.e.~240,600 km²)
361 is projected to be suitable for *B. kraussi* under one or more of the climate scenarios, increasing
362 to 3.8% (~280,300 km²) by 2070 (**S3 Table**). This includes north-east Queensland (**S6C-6E**
363 **Figs**). Horticultural production regions in northeast Queensland as far south as Townsville may
364 remain suitable for this species by 2070, although production regions in the south are likely to
365 remain unsuitable (**S6 Fig**).

366

367 ***Bactrocera musae***: Current suitable habitat for *B. musae* is predicted from the Torres Strait
368 Islands through to the Wet Tropics (**S7A-7B Figs**). The most important variable in the model

369 for *B. musae* was precipitation of the wettest quarter (78.7%) (**S1 Table**).

370

371 Projections for this species under climate change are similar to those for *B. kraussi*. Under the
372 CanESM2 scenario, 22.2% of current suitable habitat is projected to be lost by 2030, although
373 by 2070, range expansions are projected to exceed losses (**S2 Table**). However, in NorESM1-
374 M (a moderate warming scenario with little precipitation change), total range size may increase
375 by ~43.5% by 2070 (**S2 Table**). By 2030, 3.4% of Australia (i.e.~260,100 km²) is projected to
376 be suitable for *B. musae* under at least one of the climate scenarios (**S3 Table**), increasing to
377 4.2% (~300,600 km²) by 2070 (**S3 Table**).

378

379 *B. musae* mainly attacks *Musa × paradisiaca* (banana), the production areas for which are
380 located primarily in tropical and subtropical regions of the continent (**S4 Table**). The major
381 commercial growing region in the Wet Tropics is projected to remain climatically suitable for
382 this species until at least 2070 (S8 Fig).

383

384 ***Bactrocera neohumeralis***: Current suitable habitat for this species is projected to be mostly
385 confined to the Torres Strait Islands, eastern Queensland, and north eastern NSW south to
386 Wollongong (**S8A-8B Figs**). Precipitation of the wettest month (47.4%) contributed most to
387 the model for *B. neohumeralis* (**S1 Table**).

388

389 As the century progresses, considerable differences in suitable habitat are projected across the
390 six scenarios. For example, under the CanESM2 scenario, 24.2% of current suitable habitat is
391 projected to be lost by 2030, although by 2070, range expansions are projected to exceed losses
392 (**S2 Table**). Similarly, under the hot, very dry scenario simulated by GFDL-ESM2M, total
393 range size may decline by 32.4% by 2030, mostly due to contractions in the south and east,

394 although limited gains in habitat may occur in northern Australia (**S8C-8E Figs; S2 Table**).
395 By 2030, ~6.9% of Australia (i.e.~500,500 km²) is projected to be suitable for *B. neohumeralis*
396 under at least one of the climate scenarios, increasing to 14% (~1,000,100 km²) by 2070 (**S3**
397 **Table**).

398

399 Production regions in eastern Queensland and north-eastern NSW will likely remain suitable
400 for this species until at least 2070, although there is substantial uncertainty across the climate
401 scenarios. In contrast, regions along the NSW-Victorian border and further south are projected
402 to remain unsuitable for *B. neohumeralis* (**S8 Fig**).

403

404 ***Bactrocera tryoni***: Highly suitable habitat for *B. tryoni* is projected to occur along south-
405 western Western Australia, south-eastern South Australia, Victoria, and eastern Australia from
406 Cape York to NSW (**S9A-9B Figs**). Coastal zones in northern Western Australia, the Northern
407 Territory and the eastern half of Tasmania have moderate suitability (**S9A-9B Figs**). Annual
408 mean temperature (33.06%) and mean temperature of the coldest month (32.42%) had the
409 highest contributions to the model for this species (**S1 Table**).

410

411 The geographic extent of suitable habitat varies across the six climate scenarios. However, as
412 the century progresses, gains in new habitat may exceed losses under some scenarios (e.g. see
413 ACCESS1.0, MIROC5 and NorESM1-M; **S2 Table**). In contrast, under the GFDL-ESM2M
414 scenario, total range size may decline by 47.9% by 2030 (**S2 Table**), mostly due to contractions
415 in the south and east. Under the ACCESS1.0 scenario, 26.1% of current suitable habitat is
416 projected to be lost by 2030, although by 2070, range expansions are projected for some regions
417 (**S2 Table**). By 2030, 26.1% of Australia (i.e.~1,990,800 km²) is projected to be suitable for *B.*
418 *tryoni* under at least one scenario, increasing to 39.6% (~3,000,500 km²) by 2070 (**S3 Table**).

419 This includes south-west Western Australia, most of Victoria and eastern Tasmania, eastern
420 Queensland and the northern reaches of the continent (**S9C-9E Figs**).

421

422 Comparing the distribution of suitable habitat for this fly with that of its major host crops
423 indicates that key regions for these crops in the Top End of Northern Territory, eastern
424 Australia from Cape York to NSW, Victoria, and some parts of Tasmania, may remain suitable
425 for *B. tryoni* until at least 2070. Major host-plant growing regions in South Australia may also
426 remain suitable for this species until 2070 (**S9 Fig**).

427

428 ***Ceratitis capitata***: Our model suggests that suitable habitat for *C. capitata* exists throughout
429 Western Australia, the Northern Territory, the east coast of Queensland to NSW and South
430 Australia (**S10A-10B Figs**). Annual mean temperature (47.2%) and mean temperature of the
431 coldest month (46.2%) contributed most to the model for this species (**S1 Table**).

432

433 Under the future climate scenarios, the geographic extent of suitable habitat is projected to
434 increase and shift south (**S10C-10E Figs**). By 2030, 28.3% of Australia (i.e. ~2,100,400 km²)
435 is projected to be suitable for *C. capitata* under one or more scenarios (**S3 Table**), increasing
436 to 47.1% (~3,600,800 km²) by 2070 (**S3 Table**). However, under all six scenarios, 13.9%
437 (2030; ~1,000,000 km²) to 17.3% (2070; ~1,300,000 km²) of Australia is likely to be suitable
438 for *C. capitata* (**S3 Table**). Climate suitability within production regions in the south and west
439 of the continent may gradually increase for this species from 2030 to 2070 (**S10 Fig**).

440

441 ***Zeugodacus cucumis***: Suitable habitat for *Z. cucumis* is projected to occur along the northern
442 region of Western Australia and the Northern Territory, north-east Queensland, and south along
443 the east coast to NSW (**S11A-11B Figs**). Precipitation of the driest quarter (54.3%) and mean

444 temperature of the coldest quarter (36.2%) had the highest permutation importance in the model
445 for this species (**S1 Table**).

446

447 Under future climate scenarios, the geographic extent of suitable habitat is projected to
448 increase, expanding southward and inland, with most areas that are currently suitable projected
449 to remain so until at least 2070 (**S11C-11E Figs**). However, there is considerable variation
450 among projections for inland regions, indicating higher uncertainty about the future suitability
451 of these regions. For instance, under a scenario where most regions, except central Australia,
452 are projected to become drier (ACCESS1.0), total range size may increase by 68.2% by 2070
453 (**S2 Table**), with areas of expansion projected to occur in northern Western Australia, central
454 Australia, eastern Queensland and NSW (**S11C-11E Figs**). Under a warmer/wetter scenario
455 (MIROC5), a substantial westward range expansion is projected in eastern Australia (**S2**
456 **Table**). Hence, although 35.4% (~2,700,900 km²) of Australia is projected to be suitable for
457 this species under at least one scenario for 2070, a much smaller extent is suitable under all six
458 scenarios (10.3%, ~789,900 km²) (**S3 Table**).

459

460 Major commercial growing regions for host crops in Queensland and the Northern Territory
461 are projected to remain climatically suitable for this species until at least 2070 (**S11 Fig**). Other
462 major host-plant growing regions in the south and west of the continent will likely remain
463 unsuitable under the time periods considered in this study (**S11F Fig**).

464

465 **Future hotspots of pest fruit flies**

466 For each time period, we stacked habitat suitability maps for all species, to identify regions
467 most likely to contain suitable climate conditions for multiple pest species (i.e. hotspots). As
468 the century progresses, the geographic extent of suitable habitat for most of the 11 species is

469 projected to expand and shift south regardless of whether novel environments are included or
 470 excluded (**Fig 1, S12 Fig, Table 2 and S5 Table**). When regions containing novel climate are
 471 included, 31.6% of Australia (i.e. ~2,400,800 km²) is projected to be currently suitable for at
 472 least one of the 11 species. By 2070, this may increase to 52.9% (~4,000,800 km²) (**Table 2**).
 473 only a small region within Queensland’s Wet Tropics (5,621km²) is projected suitable for all
 474 11 species.

475

476 **Fig 1. Hotspot maps of habitat suitability for the 11 fruit fly species under climate change,**
 477 **when novel environments are included.** Hotspot maps of current and future habitat suitability
 478 for 11 fruit flies. Suitability was modelled with Maxent, and thresholded using the 10th
 479 percentile of suitability at training presence localities. These maps include projections under
 480 novel environments. Colours indicate the number of species for which habitat is projected to
 481 be suitable under the majority (≥ 4) future climate scenarios. Figure was created in R version
 482 3.3.3 [45] (<https://www.R-project.org/>).

483

484 **Table 2. Area (km²) and percentage (%) of Australia projected to be suitable for the 11**
 485 **fruit fly species considered in this study, under current and future climates.**

Count	Suitable area km ² (% of Australia)			
	Current	2030	2050	2070
0	5,250,277 (68.4%)	5,175,668 (67.5%)	4,567,601 (59.5%)	3,607,211 (47.0%)
1	847,090 (11.0%)	738,118 (9.6%)	887,083 (11.6%)	1,122,410 (14.6%)
2	850,401 (11.1%)	806,220 (10.5%)	1,133,009 (14.8%)	1,343,740 (17.5%)
3	176,163 (2.3%)	257,558 (3.4%)	228,976 (2.9%)	501,960 (6.5%)
4	93,709 (1.2%)	148,806 (1.9%)	248,057 (3.2%)	365,032 (4.8%)
5	121,923 (1.6%)	196,041 (2.6%)	225,006 (2.9%)	299,590 (3.9%)
6	89,766 (1.2%)	144,056 (1.9%)	141,026 (1.8%)	176,864 (2.3%)
7	101,763 (1.3%)	46,306 (0.6%)	78,803 (1.0%)	89,042 (1.2%)
8	32,385 (0.4%)	30,536 (0.4%)	37,543 (0.5%)	43,472 (0.6%)
9	57,695 (0.8%)	102,927 (1.3%)	109,316 (1.4%)	10,8250 (1.4%)
10	48,537 (0.6%)	21,554 (0.3%)	10,807 (0.1%)	9,888 (0.1%)

11	3,371 (0.0%)	5,290 (0.1%)	5,853 (0.1%)	5,621 (0.1%)
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486 Table 2. Each row of the table indicates the area (and percentage) projected to be suitable now, in 2030, 2050,
487 and 2070, for n species, where n is given in the “Count” column. Thus, the first row (with Count = 0) gives the
488 area projected to be unsuitable for all 11 species, the row with Count = 1 gives the area projected to be suitable
489 for any one of the 11 species, and the row with Count = 11 gives the area projected to be suitable for all 11
490 species.

491

492 When novel environments are excluded from maps, 31.5% of Australia is projected to be
493 currently suitable for at least one of the species, decreasing to 28% (~2,100,500 km²) by 2070
494 **(S5 Table)**. Hence, exclusion of novel environments substantially impacts the size of suitable
495 habitat (i.e., a substantial area of suitable habitat is projected to occur in areas with novel
496 climatic conditions). However, parts of the Wet Tropics bioregion is projected to remain
497 suitable for all 11 species (70 km²) and the major commercial host plants within this bioregion
498 may continue to be at risk of invasion by most or all of these high priority species.

499

500 Major commercial host plant regions along the coastal strip of south-east Queensland and
501 north-east NSW are likely to have areas that are suitable under all future scenarios for *B.*
502 *bryoniae*, *B. jarvisi*, *C. capitata* and *Z. cucumis* **(S2, S5, S10 and S11 Figs)**. Under some
503 scenarios, these regions may also be suitable for *B. halfordiae*, *B. neohumeralis* and *B. tryoni*
504 **(S4, S8 and S9 Figs)**. Some major commercial host plant regions in southern NSW and
505 Victoria are also projected to be suitable for *B. jarvisi*, *B. tryoni* and *C. capitata* under all
506 scenarios **(S5, S9 and S10 Figs)** and for *B. halfordiae*, *B. neohumeralis* and *Z. cucumis* under
507 a limited number of scenarios **(S4, S8 and S11 Figs)**.

508

509 In south-west Western Australia, major horticulture regions are likely to remain suitable for *B.*
510 *jarvisi*, *B. tryoni* and *C. capitata*, although the latter species is currently not found in this region
511 **(S5, S9 and S10 Figs)**. Commercial horticulture regions in the top-end of the Northern

512 Territory are also likely to be suitable for *B. jarvisi*, *B. kraussi*, *B. musae*, *B. tryoni* and *Z.*
513 *cucumis* under all scenarios, and *B. frauenfeldi* under some climate scenarios. Horticultural
514 regions in Tasmania are projected as suitable for *B. jarvisi*, *B. tryoni* and *C. capitata* (**S5, S9**
515 **and S10 Figs**).

516

517

518 Discussion

519 Our study suggests that the Wet Tropics bioregion has climatically suitable habitat for the
520 largest number of high priority tephritid pest species both now and as a result of climate
521 changes projected to occur through to 2070. Cape York Peninsula and the Northern Territory
522 are also likely to be vulnerable, although novel climates are projected to occur in these regions,
523 and the extrapolation of SDMs to these conditions may be unreliable. The east coast of
524 Australia is also likely to remain suitable for multiple species until at least 2070. As such, major
525 horticulture regions in north-western Australia, the Northern Territory, southern-central
526 regions of NSW, southern Victoria and north Tasmania may become increasingly suitable to
527 high priority fruit flies. Two species, *B. tryoni* (Qfly) and *C. capitata* (Medfly), are projected
528 to have suitable conditions in all states and territories of Australia, under all considered climate
529 change scenarios, until at least 2070.

530

531 Models for both Qfly and Medfly were driven primarily by temperature parameters, rather than
532 precipitation. Previous studies have identified climatic constraints on the distribution of Qfly.
533 For instance, it has been reported that Qfly pupae do not survive in the winter months in
534 Melbourne and near Sydney [56], and adults fail to emerge later than mid-April [57]. Further,
535 many subtropical sites in Queensland are marginal in winter for Qfly breeding and general

536 activity [8, 57]. As such, slight temperature increases associated with climate change are
537 projected to substantially elevate the threat that this species poses to horticultural industries
538 [58]. For instance, using data from the late 1990s, it was estimated that annual control costs for
539 apple growers around Adelaide may increase by between \$346,000 and \$1.3 million with a
540 0.5–2°C increase in temperature [58].

541

542 With the exception of Western Australia, all Australian states and territories are currently free
543 from Medfly, with market access protocols inhibiting movement into other states [21], and
544 incursions met with immediate eradication programs [13]. Our model of current habitat
545 indicates suitable conditions for Medfly around most of Australia’s coastal regions. In addition
546 to identifying suitability in the subtropical coastal fringe of Queensland, our model suggested
547 that much of the low-altitude regions in the south-east, including parts of Tasmania, are also
548 suitable. This is consistent with previous work using CLIMEX to estimate the potential
549 distribution of Medfly [25]. Competition with Qfly may be responsible for exclusion of Medfly
550 from much of Queensland [25], and similar biotic interactions may suppress the species
551 elsewhere [13]. However, Medfly may be more tolerant to low temperatures and dry summers
552 than Qfly [4], rendering Medfly the stronger competitor in areas with these conditions. Medfly
553 was recorded in Tasmania in the 1920s but reportedly failed to survive an unseasonably hot
554 and dry summer [4]. Due to their age, these records were not used to calibrate our model, yet
555 our projections indicate that Tasmania continues to have conditions suitable for this species.
556 Indeed, while strong market access protocols have excluded Qfly from Tasmania for around
557 90 years, our projections of Tasmania’s suitability were validated upon discovery of an
558 outbreak in 2018.

559

560 Allwood and Angeles [59] reported that *B. jarvisi* is recognized as a pest in north-western

561 Australia, infesting mango, guava and pomegranates (as reported in [60]). Dominiak and
562 Worsley [9] concluded that the current south-eastern range limit lies north of the Queensland-
563 NSW border ($\sim 25.5^\circ$ south), while the south-western limit lies at approximately 18° south.

564

565 However, previous analysis suggested that this species' current climatic range could extend
566 into the cooler temperate areas of southern NSW, and eastern and northern Victoria [4]. Our
567 models partly agree, indicating that suitable conditions currently occur along the east coast of
568 Victoria. This species can also withstand very warm conditions, with eggs known to be more
569 heat tolerant than those of the sympatric Qfly, surviving temperatures of 48.2°C [60]. Given
570 that these species infest many of the same hosts, competition is likely, hence eradication of
571 Qfly may result in the competitive release of *B. jarvisi*, increasing the threat it poses to
572 horticulture [4, 60]. Further, as the cultivation of *B. jarvisi* host plants expands geographically,
573 this species may increase in abundance and extend its range, potentially becoming a major pest
574 in north-western Australia [6, 36].

575

576 While widespread throughout Queensland, *Z. cucumis* currently has a restricted distribution in
577 the Northern Territory, although there is a disputed single record from northern Western
578 Australia [61]. Both Fitt [62] and the Horticultural Policy Council [4] reported that if the
579 cucurbit industry expands in the Northern Territory, the pest status of *Z. cucumis* may increase.
580 However, while the species has been trapped frequently in the Northern Territory, it has not
581 been found on cucurbits growing in this region [6]. In NSW, *Z. cucumis* appears to be currently
582 limited to regions close to the Queensland border, with rare detection as far south as Sydney
583 [61]. It has not been detected in the (former) Fruit Fly Exclusion Zone in southern NSW [37].
584 Our model also estimates the southern limit of suitable climate for this species to be around
585 Sydney. However, with climate change this may extend further southward, with parts of

586 Victoria projected to become increasingly suitable over time, depending on the climate change
587 scenario.

588

589 *Bactrocera neohumeralis* presently occurs from the western Cape York Peninsula, Queensland,
590 south to Sydney, NSW [3, 7, 37]. Our models agree that suitable conditions occur from Cape
591 York Peninsula to north of Sydney, although as climate changes, the range of this species may
592 extend southward and, under some scenarios, into parts of Victoria. Previous climatic analysis
593 also suggested that this species is well adapted to conditions on the east coast of Queensland,
594 with large populations occurring in areas north of Townsville [4]. Similar ecological
595 characteristics are shared by *B. neohumeralis* and Qfly [63], yet while Qfly is prevalent in sub-
596 tropical and temperate areas of Queensland and NSW, *B. neohumeralis* is more prevalent in
597 northern wet tropical areas [4, 5, 64]. The reason for this difference between the geographical
598 ranges of these species is unclear, as both are polyphagous and use similar host fruits for their
599 larval development [63, 64].

600

601 Our model for *B. aquilonis* indicates that suitable conditions for this species are currently found
602 in northern Queensland, although it is presently only known from north-western Australia [5].
603 The hosts of this species now include 40 commercial crops [6]. Expansion of the range of this
604 species, or the growth of host plant industries in north-western Australia may necessitate the
605 development of new monitoring, control and disinfestation procedures [60]. In addition, it has
606 been argued that if *B. aquilonis* hybridises with Qfly, and the resulting strain may have greater
607 potential for spread than *B. aquilonis* [4]. This, in turn, would require that disinfestation
608 procedures should be developed for the hybrids [60].

609

610 The Australian distribution of *B. bryoniae* ranges from the Torres Strait Islands, across northern

611 Australia, and along the east coast to north of Sydney, NSW. Our results indicate that suitable
612 habitat exists in Victoria, i.e. south of the species' known range. However, previous studies
613 have demonstrated that populations in northern NSW experience a marked decline in
614 abundance through November–January [37]. This may be explained by a decline in the fruiting
615 and flowering of native host trees, or seasonal climatic constraints that are not reflected in our
616 model [37], which may also explain their absence in Victoria.

617

618 Northern Queensland has the highest diversity of fruit flies in Australia, and some species with
619 significant economic impacts are found only in this region [7]. The distribution of *B. kraussi*,
620 *B. musae* and *B. frauenfeldi* is limited to north Queensland [3, 65], with recent trap data
621 suggesting that these species do not occur south of Townsville [7]. Royer et al. [35] predicted
622 that *B. frauenfeldi* also has suitable habitat in the Northern Territory and northern Western
623 Australia, which is also suggested by our model. The availability of hosts does not appear to
624 limit the range of *B. frauenfeldi*, which has expanded in northern Queensland due to continued
625 planting of hosts, such as mango and guava [35]. Further increases within these horticulture
626 industries in northern Queensland may increase the pest status of this fly [65].

627

628 **Model Errors and Uncertainties**

629 SDMs are useful for developing a broad understanding of how the distribution of suitable
630 habitat may be influenced by climate change. However, the output of SDMs is known to be
631 influenced by characteristics of the occurrence sample, including its size [66], sampling bias
632 [67], and spatial autocorrelation [68], as well as the extent of the study area, selection of
633 predictor variables [69], and selection of background points [70]. We addressed these issues
634 by: (1) exploring alternate settings in Maxent to optimise models and reduce overfitting that
635 may generate unreliable estimates [47]; (3) reducing the number of predictor variables by

636 assessing collinearity; and (4) critically examining response curves.

637

638 In addition, we acknowledge that the selection of a threshold for converting Maxent's
639 continuous output into binary data (typically defined as distinguishing between “suitable” and
640 “unsuitable” conditions) can be subjective and problematic. A region classified as unsuitable
641 may not be free of the pest; rather, these areas are considered less likely to support a population
642 compared with regions above the threshold. In reality, the choice of threshold is based upon a
643 comparison of the importance of false positives (FP) and false negatives (FN) [71]. For invasive
644 species, the latter may be more serious because they can result in an underestimate of the
645 geographic extent of suitable habitat, and hence, invasion risk [72]. This, in turn, can lead to
646 poor decision-making and failure to establish appropriate surveillance or containment
647 measures. Hence, in this context a precautionary approach to defining a threshold, as
648 undertaken in the present study, is warranted. However, since overprediction of suitable habitat
649 can also prove problematic (potentially leading to ineffective allocation of monitoring
650 resources), we provide continuous (unthresholded) model output, permitting stakeholders to
651 modify this threshold according to their objectives.

652

653 Sampling bias is another challenge faced when fitting correlative SDMs, particularly when
654 incorporating data from sources of incidental observations such as museums and natural history
655 collections [73]. As such, it is difficult to determine whether a species is observed in a particular
656 environment because of habitat preferences or because that region has received the largest
657 search effort [70, 73]. For presence-background approaches to habitat modelling, a target-
658 group background sampling strategy goes some way to handling biased occurrence samples
659 [74]. However, while imposing environmental bias on the background counteracts similar bias
660 in the occurrence sample, this strategy may increase the extent of novel environments to which

661 the model must be extrapolated.

662

663 While SDMs consider exposure to climate change, species responses may also include
664 microevolution [75] or plasticity [76]. As accessibility to genomic data increases, and
665 experiments on plasticity are conducted, SDM output can be refined [77]. In addition, as mean
666 conditions change, so too will the distribution and magnitude of extremes. Presently, there has
667 been little work undertaken to assess how different fruit fly species tolerate extreme weather
668 events such as heatwaves and moisture stress.

669

670 We also note that our analysis does not take into consideration the potential necessity for
671 horticultural industries to shift geographically to adapt to climate change. Analysing potential
672 shifts in climatic suitability for horticultural crops is complicated by our capacity to modify the
673 environment (e.g. through irrigation), and thus was beyond the scope of this study.

674

675

676 Conclusions

677 Surveillance activities, pre- and post-harvest treatment, and control activities for fruit flies
678 present a substantial cost to Australia's horticultural industries [2, 4, 14]. Climate change is
679 likely to alter the distribution of suitable habitat for these species, and this could have
680 ramifications for Australia's horticultural industries. Our analysis highlights that the major
681 horticultural production regions are likely to remain suitable for multiple economically
682 important fruit fly species as climate changes. Furthermore, given that knowledge of current
683 species distributions remains the basis for market access decisions, the potential for range shifts
684 to occur is of critical interest to horticultural industries.

685

686 Our model projections identify geographic regions likely to be suitable for 11 high priority,
687 economically important pest fruit fly species, now and in the future. Outputs from this study
688 provide guidance to pest managers, such that they can assess pest risks and design appropriate
689 ongoing surveillance strategies. Our results emphasize the importance of vigilance and
690 preparedness across Australia, to prevent further range expansion of these 11 species, and
691 underscore the need for ongoing research and development into monitoring, control, and
692 eradication tools.

693

694

695 Supporting Information

696

697 **S1-11 Figs. Climatic habitat suitability for 11 tephritid fruit flies under various future**
698 **climate scenarios.** (1) *Bactrocera aquilonis* (2) *Bactrocera bryoniae* (3) *Bactrocera*
699 *frauenfeldi* (4) *Bactrocera halfordiae* (5) *Bactrocera jarvisi* (6) *Bactrocera kraussi* (7)
700 *Bactrocera musae* (8) *Bactrocera neohumeralis* (9) *Bactrocera tryoni* (10) *Ceratitidis capitata*.
701 (11) *Zeugodacus cucumis*. (A) current habitat suitability modelled using Maxent – values close
702 to zero represent areas with low climatic suitability while values closer to one indicate higher
703 climatic suitability; (B) areas considered “suitable” (i.e., with habitat suitability values above
704 the 10th percentile at training presence sites, shown in red); (C, D, E) agreement about the
705 suitability of habitat for the species across six climate scenarios for 2030, 2050 and 2070,
706 respectively; (F) the location of Australian occurrence records of the species, based on
707 specimens from natural history collections, literature and State Government trapping programs,

708 and major commercial horticultural hosts, according to the Australian Horticulture Statistics
709 Handbook (HSHB; www.horticulture.com.au).

710

711 **S12 Fig. Hotspot maps of habitat suitability for the 11 fruit fly species under climate**
712 **change, when novel environments are excluded.** Hotspot maps of current and future habitat
713 suitability for 11 fruit flies with regions containing novel environments considered unsuitable.
714 Suitability was modelled with Maxent, and thresholded using the 10th percentile at training
715 presence localities. Colours indicate the number of species for which habitat is predicted to be
716 suitable under the majority (≥ 4) future climate scenarios. Figure was created in R version
717 3.3.3[1] (<https://www.R-project.org/>).

718

719 **S1 Table. Model performance and bioclimatic variables used to investigate the suitability**
720 **of habitat for tephritid fruit fly species.** AUC value indicates the area under the receiver
721 operating characteristic curve (average of 5 cross-validated replicates), which was used to
722 evaluate model performance; SD (standard deviation); and HPI (highest permutation
723 importance, %) of bioclimatic variables contributing to the model where BIO01: annual mean
724 temperature, BIO02: mean diurnal range; BIO03: isothermality; BIO06: minimum temperature
725 of the coldest month; BIO07: temperature annual range; BIO11: mean temperature of the
726 coldest quarter; BIO13: precipitation of wettest month; BIO14: precipitation of the driest
727 month; BIO16: precipitation of the wettest quarter; BIO17: precipitation of the driest quarter
728 and BIO19: precipitation of the coldest quarter.

729

730 **S2 Table. Projected changes in the area of suitable habitat for all 11 fruit fly species,**
731 **under six future climate scenarios, relative to the current period.** (1) *Bactrocera aquilonis*
732 (2) *Bactrocera bryoniae* (3) *Bactrocera frauenfeldi* (4) *Bactrocera halfordiae* (5) *Bactrocera*

733 *jarvisi* (6) *Bactrocera kraussi* (7) *Bactrocera musae* (8) *Bactrocera neohumeralis* (9)
734 *Bactrocera tryoni* (10) *Ceratitidis capitata* (11) *Zeugodacus cucumis*. For each species, the first
735 column indicates the GCM (Global Climate Model) for three time periods 2030, 2050 and
736 2070. Other columns: % Lost refers to the percentage of currently suitable habitat projected to
737 become unsuitable in the future; % Gained refers to the percentage of future suitable habitat
738 that is in areas currently unsuitable; Range Changed refers to the change (%) between the size
739 of current and future suitable habitat (positive numbers indicate an increase in range size,
740 negative numbers indicate a decrease).

741

742 **S3 Table. Area (km²) and percentage of Australia projected to be suitable for 11 fruit flies**
743 **under six future climate scenarios.** In the column ‘Climate scenarios’, 0 refers to the area
744 projected to be unsuitable across all six scenarios; 1 refers to the area projected to be suitable
745 under any one of the six scenarios...6 refers to the area projected to be suitable under all six
746 scenarios.

747

748 **S4 Table. Major commercial fruits and vegetables host species to the Australian**
749 **Horticulture Statistics Handbook (HSHB; www.horticulture.com.au).** Pest status is based
750 on Hancock et al³, where “major” indicates that there have been many records of the fly
751 infesting that host.

752

753 **S5 Table. Area (km²) and percentage (%) of Australia projected to be suitable for the 11**
754 **fruit fly species considered in this study, when novel environments have been excluded.**
755 Each row of the table indicates the area (and percentage) projected to be suitable now, in 2030,
756 2050, and 2070, for *n* species, where *n* is given in the “Count” column. Thus, the first row (with
757 Count = 0) gives the area projected to be unsuitable for all 11 species, the row with Count = 1

758 gives the area projected to be suitable for any one of the 11 species, and the row with Count =
759 11 gives the area projected to be suitable for all 11 species. Values shown here apply when
760 cells with novel environmental conditions are considered unsuitable.

761

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769

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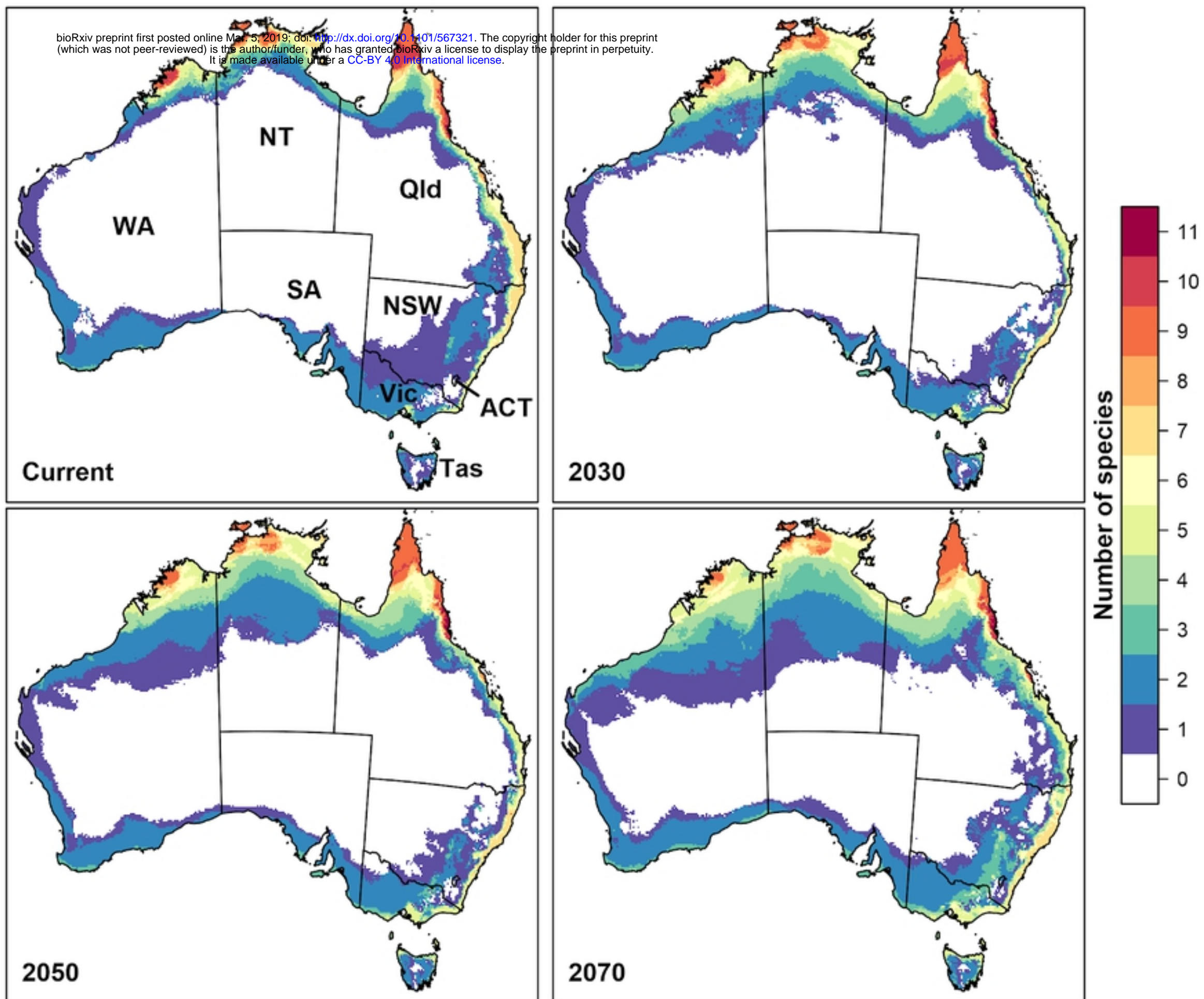
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Figure