Predicted the impacts of climate change and extreme-weather events on the future

distribution of fruit bats in Australia

Vishesh L. Diengdoh[1], e: vishesh.diengdoh@utas.edu.au, ORCID: https://orcid.org/0000-0002-0797-9261

Stefania Ondei[1] - e: stefania.ondei@utas.edu.au

Mark Hunt[1,3] - e: M.Hunt@utas.edu.au

Barry W. Brook[1,2] - e: barry.brook@utas.edu.au

[1]School of Natural Sciences, University of Tasmania, Private Bag 55, Hobart TAS 7005 Australia

[2]ARC Centre of Excellence for Australian Biodiversity and Heritage, Australia

[3]National Centre for Future Forest Industries, Australia

Corresponding Author: Vishesh L. Diengdoh

Acknowledgements

Conflict of Interest

None.

Author Contributions

VLD proposed and designed the study, analysed the data, and wrote the manuscript. SO contributed significantly to the study design and writing of the manuscript. MH contributed to the writing of the manuscript. BWB contributed significantly to the study design and writing of the manuscript.

Biosketch

VLD is a PhD student at the Dynamics of Eco-Evolutionary Patterns (DEEP) research group at the University of Tasmania, Australia. He is interested in understanding how land-use and land-cover change and climate change impact pollinators.

1   **Abstract**

2   *Aim*

3   Fruit bats (Megachiroptera) are important pollinators and seed dispersers whose distribution

4   might be affected by climate change and extreme-weather events. We assessed the potential

5   impacts of those changes, particularly more frequent and intense heatwaves, and drought, on

6   the future distribution of fruit bats in Australia. We also focus a case study on Tasmania, the

7   southernmost island state of Australia, which is currently devoid of fruit bats but might serve

8   as a future climate refugium.

9   *Location*

10   Australia (continental-scale study) and Tasmania.

11   *Methods*

12   Species distribution modelling was used to predict the occurrence of seven species of fruit

13   bats, using an ensemble of machine-learning algorithms. Predictors included extreme-weather

14   events (heatwave and drought), vegetation (as a proxy for habitat) and bioclimatic variables.

15   Predictions were made for the current-day distribution and future (2050 and 2070) scenarios

16   using multiple emission scenarios and global circulation models.

17   *Results*

18   Changes in climate and extreme-weather events are forecasted to impact all fruit-bat species,

19   with the loss and gain of suitable areas being predominantly along the periphery of a species'

20   current distribution. A higher emission scenario resulted in a higher loss of areas for Grey-

21   headed flying fox (*Pteropus poliocephalus*) and Spectacled flying fox (*P. conspicillatus*) but

22   a higher gain of areas for the Northern blossom bat (*Macroglossus minimus*). The Grey-

23   headed flying fox (*Pteropus poliocephalus*) is the only study species predicted to potentially

24   occur in Tasmania under future scenarios.

25   *Main conclusions*

26   Fruit bats are likely to respond to climate change and extreme weather by migrating to more

27   suitable areas, including regions not historically inhabited by those species such as

28   Tasmania—possibly leading to human-wildlife conflicts. Conservation strategies (e.g.,

29   habitat protection) should focus on areas we found to remain suitable under future scenarios,

30   and not be limited by state-political boundaries.

31   **Keywords**

32   Climate change, climate refugia, extreme weather, Macroglossus, Megachiroptera, Pteropus,

33   species distribution models.

34 **Introduction**

35 The projected increase in global temperature and the frequency and intensity of extreme-

36 weather events (IPCC 2014) is a cause of concern for biodiversity protection worldwide, as

37 these changes are observed and predicted to impact the diversity, distribution and mortality of

38 various taxa (McKechnie and Wolf 2010; Newbold 2018; Parmesan and Yohe 2003; Titley

39 et al. 2021; Welbergen et al. 2007). Species are expected to respond to increasing

40 temperatures and extreme weather by shifting their distribution towards more suitable areas

41 (Maxwell et al. 2019; Stillman 2019), likely including new habitats and geopolitical areas

42 (Titley et al. 2021). Range shifts can result in changes in community structure and ecosystem

43 processes which can have positive and negative implications; assessing these changes and

44 implications is essential for developing conservation policies (Wallingford et al. 2020).

45 Fruit bats (Megachiroptera) are an important climate-impact case study. They are a visually

46 striking flying mammal (easily noticed and forming large colonies) that play a critical

47 ecological role in pollination and seed dispersal and can carry large pollen loads and seeds

48 over long distances (Fleming et al. 2009). Their regional diversity and distributional range are

49 expected to be impacted by climate change across several areas within their global extent,

50 which includes Africa, Nepal, Southeast Asia, and Australia (Arumoogum et al. 2019;

51 Hughes et al. 2012; Thapa et al. 2021; Welbergen et al. 2007). Extreme weather events have a

52 particularly strong impact on flying foxes (*Pteropus* spp.), with heatwaves causing many

53 recorded mass-mortality events (Kim and Stephen 2018; Welbergen et al. 2014; Welbergen et

54 al. 2007).

55 In Australia, correlative species distribution models (SDM) have been used, in a few cases, to

56 assess the impacts of climate change on fruit bats, but either failed to account for changes in

57 extreme weather (see Graham et al. 2019) or did not use species-specific temperature

58   thresholds (see Morán☐Ordóñez et al. 2018). The latter is a potentially problematic limitation

59   because temperatures above 42 °C are considered as heatwaves for flying foxes (Ratnayake et

60   al. 2019; Welbergen et al. 2007) while for other species such as bettongs (genus *Bettongia)*

61   temperatures above 28 °C are considered as heatwaves (Bateman et al. 2012). To date, no

62   study has combined projections of future climate with the estimated future frequency and

63   intensity of extreme-weather events (heatwaves and drought) to predict the potential changes

64   in the distribution of fruit bats in Australia—yet this arguably constitutes among the greatest

65   threats to Megachiroptera and bats in general; changes in temperature and precipitation, lack

66   of availability of water, and natural abiotic factors such as weather and fire can impact the

67   survivability and distribution of bats (O'shea et al. 2016; Sherwin et al. 2013).

68   Fruit bats could respond to climate change and extreme-weather events by shifting their

69   distribution to more suitable areas, because they are highly agile and often travel large

70   distances in search of resources (Roberts et al. 2012; Tidemann and Nelson 2004), with a

71   track record of being able to colonise previously uninhabited areas (Boardman et al. 2020;

72   Parris and Hazell 2005; Westcott and McKeown 2014). In this regard, it is also worth

73   considering whether Tasmania, the southernmost island state of Australia, which historically

74   lacks fruit bats, might be suitable under future climate change. Colonisation by fruit bats to

75   previously uninhabited areas can have significant consequences, as they are a frequent

76   subject of human-wildlife conflicts (Roberts et al. 2012; Tait et al. 2014).

77   This study aims to assess the potential impacts of climate change and extreme-weather events

78   (heatwaves and drought) on fruit bats in Australia, with particular emphasis on the suitability

79   of Tasmania as a future climate refugium. We used correlative SDMs and an ensemble of

80   machine-learning algorithms (hereafter: algorithms) to estimate the occurrence of fruit bats

81   under current and future climate scenarios (multiple years, emission scenarios and global

82   circulation models). We highlighted which existing geographical areas will become

83   climatically unsuitable and/or new areas suitable for fruit bats in the future and recommend

84   potential strategies to help conserve fruit bats in Australia.

85   **Methods**

86   *Study species*

87   Australia has 13 species of fruit bats (Hall and Richards 2000). We downloaded records of

88   species occurrence (presence) from Atlas of Living Australia (Atlas of Living Australia

89   2020). Records were limited to those from 1960 and onwards and classified as 'human

90   observation'. We removed duplicate records based on latitude and longitude and dubious

91   records (e.g., outliers well outside the known distribution ranges).

92   We selected those species reported as present in at least 20 different cells of 0.05° spatial

93   resolution (∼ 5 km). Consequently, the Grey-headed flying-fox (*Pteropus poliocephalus*),

94   Little red flying-fox (*P. scapulatus*), Black flying-fox (*P. alecto*), Spectacled flying-fox (*P.*

95   *conspicillatus*), Common blossom bat (*Syconycteris australis*), Northern blossom bat/Dagger-

96   toothed long-nosed fruit bat (*Macroglossus minimus*), and the Eastern tube-nosed bat

97   (*Nyctimene robinsoni*) were modelled in this study; the other species did not have sufficient

98   data. The IUCN Red List (IUCN 2020) lists only the Grey-headed flying fox as vulnerable

99   (Lunney et al. 2008) and the Spectacled flying fox as endangered (Roberts et al. 2020), while

100   the other species are classified as 'least concern'.

101   Presence data was reduced to a single observation per grid cell. Pseudo-absences were

102   generated using the target☐group method (Phillips et al. 2009) as it has been shown to

103   robustly handle sampling bias, especially concerning visitation (Fithian et al. 2015). The

104   method consists of generating pseudo-absences for each species by using the presence points

105   of other fruit bats.

106   *Study area*

107   Fruit bats occur along the coastal margin of the Australian continent, and in some inland

108   regions (Hall and Richards 2000). They are found across a range of habitats, including

109   rainforests, savannas, and urban areas (Hall and Richards 2000; Tait et al. 2014; Westcott

110   2010). Restricting the geographic extent using a geographical criterion can improve model

111   performance (Acevedo et al. 2012). We examined habitat suitability across the Australian

112   continent, with the exclusion of desert regions, as identified using a Köppen-Geiger climatic

113   layer (Beck et al. 2018), because we assumed it is unlikely that these regions will be suitable

114   for fruit bats due to their high temperatures and extreme range. We also used land-cover data

115   (version 2.1; Lymburner et al. 2015) to mask out land-cover categories we do not expect fruit

116   bats to occupy: extraction sites, salt lakes and alpine grassland.

117   *Study predictors*

118   To model species occurrence, we selected heatwave, drought, vegetation, and bioclimatic

119   variables as predictors. These predictors all have a spatial resolution of 0.05° ($\sim$ 5 km).

120   Bioclimatic variables and vegetation were resampled using the bilinear interpolation method

121   and nearest neighbour method, respectively, to match the spatial resolution of the heatwave

122   and drought predictors. Resampling was carried out using the *raster* R package (Hijmans

123   2020).

124   Heatwave refers to the number of days when maximum or minimum temperature is equal to

125   or greater than 42 °C are tallied in both the historic and projected future 30-year daily time

126   series and averaged annually over the 30-years. Drought refers to the number of months

127   falling below the historic 10th percentile rainfall total were counted in both the historic and

128   projected future 30-year monthly time series and averaged annually over the 30-years.

129   Heatwaves have caused multiple mortality events in flying foxes (*Pteropus* spp.; Kim and

130   Stephen 2018; Welbergen et al. 2014; Welbergen et al. 2007). We are unaware of similar

131   events being recorded in other, rarer (less conspicuous) fruit-bat species– *Nyctimene* spp.,

132   *Macroglossus* spp., and *Syconycteris* spp., however, we assumed these fruit bat genera to

133   have the same temperature threshold as flying foxes (*Pteropus* spp.). Drought can impact the

134   availability of foraging resources (Lučan et al. 2016) which in turn could influence the

135   occurrence of fruit bats. Heatwave and drought variables were downloaded from Climate

136   Change in Australia (https://www.climatechangeinaustralia.gov.au; Clarke et al. 2011;

137   Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Bureau of

138   Meteorology 2020; Whetton et al. 2012). Given the influence of heatwaves and drought on

139   fruit bats, we selected bioclimatic variables that were a direct measure of temperature and

140   precipitation: minimum, maximum, and mean temperature and precipitation of different

141   months and quarters (see Appendix S1 Table S1.1 in Supporting Information). Bioclimatic

142   variables were downloaded from WorldClim (version 2.1; https://www.worldclim.org; Fick

143   and Hijmans 2017).

144   Vegetation is important in the selection of foraging and roosting sites for fruit bats (Tidemann

145   et al. 1999). We assumed vegetation to be a constant predictor under current and future

146   scenarios due to lack of data on its future distribution, although it is likely to eventually track

147   climate shifts too. Vegetation data (major groups) were downloaded from the National

148   Vegetation Information System (version 5.1; Australian Government Department of

149   Agriculture Water and the Environment 2018). These data consisted of thirty-three vegetation

150   classes, which were reduced to fourteen macro classes (see Appendix S1 Table S1.2).

151   To account for the influence of climate models and emission scenarios on SDMs (Brun et al.

152   2020; Goberville et al. 2015; Thuiller et al. 2019), we selected multiple global circulation

153   models (GCMs) and representative concentration pathways (RCP) to model species

154   occurrence for 2050 and 2070. The bioclimatic and extreme-weather-events data sources had

155   different GCMs available, limiting our choice to GCMs common across the two data sources.

156   This left three GCMs: Australian Community Climate and Earth System Simulator 1.0

157   (ACCESS 1.0; Bi et al. 2013), Hadley Centre Global Environment Model Carbon Cycle

158   (HadGEM2-CC; Collins et al. 2011), and the Model for Interdisciplinary Research on

159   Climate (MIROC5; Watanabe et al. 2010). We selected RCP 4.5 (Thomson et al. 2011) and

160   8.5 (Riahi et al. 2011) because they represented medium- and high-emission scenarios

161   respectively, and best match the current emissions trajectory. The bioclimatic variables from

162   the multiple GCMs and RCPs were downloaded from WorldClim (http://worldclim.com/;

163   version 1.4; Hijmans et al. 2005).

164   *Training data*

165   The training data were biased to pseudo-absences with presence to pseudo-absence ratio set

166   to a maximum of 1:10. Pseudo-absences points were selected using a stratified random

167   method to ensure an adequate number of vegetation class (the only factorial predictor) were

168   represented, and thereby result in better training data. The training data for each species will

169   be made public via figshare with the following DOI

170   https://doi.org/10.6084/m9.figshare.14583282. However, currently, the data can be shared

171   privately on request.

172   *Variable selection*

173   We reduced the number of predictors by removing correlated variables using a threshold

174   value of 0.7 (Dormann et al. 2013). We used the *findCorrelation* function in the *caret* R

175   package (Kuhn 2020) to remove, for each pair of highly correlated variables, the one with the

176   largest mean absolute correlation. Instead of using all the non-correlated predictors to fit the

177   models, we created a list of all possible combinations of three non-correlated bioclimatic

178   predictors and included heatwave, drought, and vegetation predictors since they were not

179   strongly correlated to each other or any of the climate variables. We constrained any given

180   approach to a maximum of six predictors, to keep the models relatively simple. This resulted

181   in a set of four different groups of predictors/candidate models for each species (see

182   Appendix S1 Table S1.3).

183   *Cross-validation*

184   We used repeated 70/30% training/test cross-validation splits with 50 repeats for algorithm

185   tuning/optimisation, selecting predictor/candidate models for each species, and calculating

186   the variable importance. Accuracy was evaluated using Area Under the Receiver Operating

187   Characteristic Curve (AUC) and True Skill Statistic (TSS) (Allouche et al. 2006) of the test

188   (hold-out) data. The algorithms used in the study include random forest (RF), classification

189   and regression trees (CART), neural network (NN), stochastic gradient boosting (GB),

190   penalised generalized linear model (GLM), penalised multinomial regression (MR) and

191   flexible discriminant analysis (FDA). These algorithms were selected as they are commonly

192   available in species distribution modelling R packages (see Naimi and Araújo 2016; Schmitt

193   et al. 2017). Cross-validation was implemented using the unified *caret* and *caretEnsemble* R

194   packages (Deane-Mayer and Knowles 2019; Kuhn 2020). The accuracy metrics achieved by

195   the predictor/candidate models are provided in the supplementary material (see Appendix S1

196   Table S1.3).

197   *Species occurrence models*

198   Occurrence models were then re-fitted to the full dataset using the best predictor/candidate

199   models derived from the cross-validation step. We also assessed the partial dependence plots

200   of each algorithm and then averaged them (unweighted) using the *pdp* r package (Greenwell

201   2017). Given that SDMs are influenced by algorithms and climate models (Brun et al. 2020;

202   Thuiller et al. 2019) we selected an ensemble modelling method. An ensemble algorithm

203   averages the prediction of structurally different algorithms and could potentially overcome

204   uncertainty in model selection and improve prediction accuracy by reducing variance and

205   bias (Dormann et al. 2018). As such, we averaged the algorithms using an unweighted

206   method and assessed the AUC and TSS (Allouche et al. 2006) of the final ensemble model.

207   Future-occurrence predictions were made for each species per year per emission scenario per

208   climate model and then ensembled (unweighted) per year per emission scenario for each

209   species.

210   *Species presence-absence models*

211   We used the sensitivity☐specificity sum maximisation approach (Liu et al. 2005) to select the

212   optimal suitability threshold for transforming the probabilistic ensemble occurrence models

213   to binary (presence and absence representations). Using the prediction under current climatic

214   conditions as a reference, we determined which areas (i.e., number of occupied grid cells)

215   will be stable, lost, or gained under future climatic scenarios. Stable areas are those that

216   remain climatically suitable or unsuitable under current and future scenarios. Lost areas are

217   those currently suitable but predicted to become unsuitable under future scenarios. Gained

218   areas are those that are currently unsuitable but predicted to become suitable under future

219   scenarios. We additionally assessed the presence of a species under different climate types.

220   We assess the presence of a species under current conditions and future scenarios using the

221   present and future climate type by Beck et al. (2018), respectively.

222   The study method is additionally described using the Overview, Data, Model, Assessment

223   and Prediction (ODMAP) protocol (Zurell et al. 2020; see Appendix S2). All the analyses

224   were done using R software (R Core Team 2020).

225   **Results**

226   The ensemble models for the Grey-headed flying fox, Spectacled flying fox, and Northern

227   blossom bat under current climatic conditions achieved high descriptive accuracy (Table 1;

228   Fig.1). The models for the Little red flying fox, Black flying fox, Eastern tube-nosed, and

229   Common blossom bat achieved lower accuracy metrics (AUC 0.7-0.8 and TSS 0.2-0.4)

230   during cross-validation, and as a result, we did not predict the occurrence for these species

231   (see Appendix S1 Table S1.3). Predictions for climate-change scenarios were thus made for

232   only three species: Grey-headed flying fox, Spectacled flying fox, and Northern blossom bat

233   (Fig. 2). The predicted ensemble occurrence models for the Grey-headed flying fox,

234   Spectacled flying fox, and Northern blossom bat will be made publicly available as GeoTiff

235   images via https://doi.org/10.6084/m9.figshare.14583282.

236   Overall, mean temperature of wettest quarter, precipitation of warmest quarter, and mean

237   temperature of driest quarter, were the most important predictors for the Grey-headed flying

238   fox, Spectacled flying fox, and Northern blossom bat models, respectively (see Appendix S1

239   Table S1.4). The extreme weather-event predictors (heatwave and drought) were among the

240   top five important variables for all the models. The vegetation class of non-native vegetation

241   was the most important for the Grey-headed flying fox and Spectacled flying fox, while the

242   vegetation class Eucalypt was the most important for the Northern blossom bat (see

243   Appendix S1 Table S1.4).

244   Based on the partial-dependence plots we found, the probability of occurrence of the Grey-

245   headed flying fox decreases with the increasing number of days of drought (range from 0.5 to

246   1.4 days). However, its occurrence increases with the number of days of heatwaves (0.0 to

247   0.4 days) up to 0.3 days after which it decreases (see Appendix S1 Fig. S1.1). For the

248   Spectacled flying fox, the occurrence decreases with the increasing number of days of

249   drought (0.5 to 1.4 days) and heatwave (0.0 to 0.5 days; see Appendix S1 Fig. S1.2) while for

250   the Northern blossom bat, the occurrence increases and decreases with the increasing number

251   of days of drought (0.5 to 1.3 days) and heatwave (0.0 to 0.5 days), respectively (see

252   Appendix S1 Fig. S1.3). The vegetation types of Acacia, Mallee, and Rainforest were

253   associated with a lower probability of occurrence of the Grey-headed flying fox, while no

254   major differences were detected among the other vegetation types (Appendix S1 Fig. S1.1).

255   Eucalypt and non-native vegetation types have the highest positive influence on the

256   Spectacled flying fox, which has a low probability of occurrence in all the other vegetation

257   types (Appendix S1 Fig. S1.2). Eucalypt, rainforest and other shrublands have the highest

258   positive influence on the Northern blossom bat, while Acacia and Grassland vegetation are

259   predicted to have the least influence (Appendix S1 Fig. S1.3).

260   The severity of impacts of climate change and extreme weather events varied between

261   species, and so did the extent of areas lost and gained, which depended on the year and

262   emission scenario considered (Fig. 3). As expected, areas lost and gained were, overall,

263   predicted to occur along the edges of a species' current distribution range (Fig. 3). For the

264   Grey-headed flying fox and Spectacled flying fox, the percentage of areas lost was predicted

265   to be higher in the year 2070 than 2050 and higher under 8.5 than 4.5 emission scenario.

266   Conversely, for the Northern blossom bat, the percentage of areas lost was predicted to be

267   higher in the year 2050 than 2070 and higher under 4.5 than 8.5 emission scenario (see

268   Appendix S1 Table S1.5). For the Grey-headed flying fox and Northern blossom bat, the

269   percentage of areas gained was forecasted to be higher in the year 2070 than 2050 and under

270   8.5 than 4.5 emission scenario. However, for the Spectacled flying fox, the percentage of

271   areas gained was predicted to be higher in the year 2050 than 2070 and higher under 4.5 than

272   8.5 emission scenario (Appendix S1 Table S1.5). The binary (presence and absence) models

273   for the Grey-headed flying fox, Spectacled flying fox, and Northern blossom bat will be made

274   publicly available as GeoTiff images via https://doi.org/10.6084/m9.figshare.14583282.

275   Under current conditions, the occurrence of the Grey-headed flying fox was found to be

276   highest in temperate no dry season warm-summer climate and temperate no dry season hot

277   summer climate which are found along the southeast of Australia including Tasmania (see

278   Appendix S1 Table S1.6; climate descriptions are based on Köppen-Geiger climate

279   classification, see Beck et al. 2018). Under future scenarios, the occurrence of the Grey-

280   headed flying fox increases in temperate no dry season hot summer climate but decreases in

281   temperate dry summer warm summer and arid steppe cold climate (see Appendix S1 Table

282   S1.6). The occurrence of the Spectacled flying fox is highest in tropical and temperate dry

283   winter hot summer climate under current conditions. These climates are found in the north

284   and northeast of Australia. However, this species is not predicted to occur in temperate dry

285   winter hot summer climate under future scenarios (see Appendix S1 Table S1.6). The

286   occurrence of the Northern blossom bat is highest in tropical savannah climate under current

287   conditions and future scenarios (see Appendix S1 Table S1.6). Tropical savanna is found in

288   northern Australia.

289   Of the species studied, only the Grey-headed flying fox is predicted to occur in Tasmania and

290   under current conditions and future scenario (Fig. 2a-d). The Grey-headed flying fox is also

291   predicted to occur across the southwest of Australia, which is also devoid of fruit bats, under

292   current conditions. However, unlike Tasmania, the occurrence in southwest Australia is

293   predicted to decrease with increasing emission scenario and year (Fig. 2a-d).

294   **Discussion**

295   Fruit bats are important vertebrate pollinators (Fleming et al. 2009) but are threatened by

296   climate change and extreme weather events (O'shea et al. 2016; Sherwin et al. 2013). We

297   assessed the impacts of those factors on the occurrence and abundance of fruit bats in

298   Australia using correlative SDMs with an emphasis on Tasmania as a potential future

299   refugium under climate change. Of the seven species studied, we obtained reliable models

300   (under current conditions) for only the Grey-headed flying fox, Spectacled flying fox, and

301   Northern blossom bat, and consequently, future distribution was modelled for these three

302   species. We found that the predicted impacts varied between species, year, and emission

303   scenarios in complex ways. Of the three species with forecasts, the Grey-headed flying fox,

304   the only one currently found in temperate areas, was predicted to have suitable conditions in

305   Tasmania under both current and future scenarios.

306   The overall loss and gain of areas along the edges of species distributional ranges are, in large

307   part, driven by the predicted expansion of hotter climate types into cooler climates in

308   Australia (see Beck et al. 2018). In general, populations along range boundaries are likely to

309   be more sensitive to climate change and extreme weather than those within the core

310   (Parmesan et al. 2000). Tidemann and Nelson (2004) have suggested that the northern edge

311   of the Grey-headed flying fox has already contracted south due to climate change and our

312   results indicate that climate change and extreme weather events will further exacerbate this

313   process. We were unable to find comparative studies for our findings of the Spectacled flying

314   fox and Northern blossom bat.

315   The Grey-headed flying fox is found in warm temperate to tropical climates (Parris and

316   Hazell 2005), while the Spectacled flying fox is found in the wet tropics (Tait et al. 2014).

317   This could explain why temperate dry summer climate types and temperate hot summer

318   climate are found to be associated with a decrease in suitability for the Grey-headed flying

319   fox and Spectacled flying fox, respectively. The biogeographic region that a bat species

320   occupies can influence its response to climate change (Rebelo et al. 2010).

321   Our predictions indicate that the Grey-headed flying fox could be supported by the climatic

322   conditions that exist today in Tasmania, even though they are currently not found on the

323   island. Tasmania's glacial history might have limited the availability of suitable habitat in the

324   past, preventing flying foxes from establishing permanent colonies on the island (Driessen et

325   al. 2011). However, as species can shift their distribution as a response to climate change

326 (Parmesan and Yohe 2003; Titley et al. 2021), particularly endothermic species, such as bats,

327 that track their niche (Araújo et al. 2013), it is plausible that future climate and extreme

328 weather events and the reduction of suitable habitat in their original distributional range could

329 drive the Grey-headed flying fox to Tasmania, despite the 250 km wide oceanic barrier of

330 Bass Strait. Indeed, apparent vagrants have occasionally been recorded on the Bass Strait

331 islands (Driessen 2010).

332 Shifting the probability density or total range of a species' distribution as a response to

333 climate change is possible when gradual changes in ambient temperature allow for

334 adjustment of their physiology and behaviour to new conditions. However, this might not be

335 feasible for extreme-weather events such as heatwaves (Bondarenco et al. 2014). This may

336 result in a situation where flying foxes need human-assisted migration to established in places

337 such as Tasmania, to safeguard their population viability. This, in turn, gets to the deeper

338 social question of whether the general public would be willing to tolerate climate-driven

339 'refugees', a term applicable to animals as well (Derham and Mathews 2020), colonising new

340 habitats—such as Tasmania—naturally or through human assistance.

341 The management of species moving into new geopolitical areas will likely depend on their

342 ecological and socio-economic values (Scheffers and Pecl 2019). Fruit bats can contribute to

343 pollination (a key ecosystem service) in Tasmania and as nocturnal mammal species, they are

344 unlikely to compete with diurnal nectarivorous and frugivorous birds, although they could

345 reduce resource availability (Westcott and McKeown 2014). However, bats are known

346 carriers of diseases, e.g., Hendra virus (Martin et al. 2018), and as such have been persecuted

347 (Hughes et al. 2007; MacFarlane and Rocha 2020) and are a frequent subject of human-

348 wildlife conflicts (Roberts et al. 2012; Tait et al. 2014). This would make their management

349 in new locations a complex and challenging task. In this context, we advocate that, whilst *in-*

350 *situ* protection should be the primary aim of all conservation efforts, there remains a need to

351   speculate on, model, and discuss potential *ex-situ* conservation strategies. Our results

352   underscore the importance of implementing conservation strategies focused on areas and

353   climatic zones commonly suitable under all predicted scenarios (Fig. 3), which do not respect

354   geopolitical boundaries.

355   The unreliable models that resulted from the available occurrences for the Little red flying

356   fox, Black flying fox, Eastern tube-nosed and Common blossom bat were probably due to a

357   combination of sampling inadequacy and/or bias, biotic interactions, and spatial scale. The

358   number and location of presence points can influence model accuracy (van Proosdij et al.

359   2016; Wisz et al. 2008), limiting the ability to model the distribution of species with few

360   presence points. Occurrence records could also be out of equilibrium with their current

361   environment due to recent past human impacts, such as land-use and land-cover change,

362   which can also degrade model outcomes (Dormann 2007). Finally, the spatial scale of the

363   data used was ~5 km, which is relatively coarse and might fail to represent important habitat

364   characteristics for some species, as sensitivity to scale can depend on the species attributes

365   (Dormann 2007).

366   **Conclusion**

367   Our study found climate change and associated changes in extreme-weather events to have

368   generally detrimental, but different impact on fruit-bat species. Although no fruit bats are

369   currently found in the southernmost part of Australia (Tasmania), this large island is found to

370   be climatically suitable for the Grey-headed flying fox, now and in the future. Fruit bats

371   could respond to climate change and extreme-weather events by migrating to more suitable

372   areas or do so via human-assisted migration, to safeguard their population viability. Both

373   instances raise challenging socio-political questions that would benefit from discussion and

374   debate now, rather than at some future crisis point. Although our study assessed the impacts

375 of climate change and extreme weather events of fruit bats in Australia, we are unaware of

376 how these changes would affect the Spectacled flying fox and the Northern blossom bat

377 which are also found in Southeast Asia and on Pacific Islands (Francis et al. 2008; Roberts et

378 al. 2020). Future studies should consider assessing the impacts of climate change and extreme

379 weather events across a species entire distribution range. Future studies should also consider

380 collecting additional field information to obtain more reliable models, mapping movement

381 patterns for fruit bats under climate change and developing mechanistic (physiology-based)

382 SDMs to further improve the focus of conservation efforts.

383 **References**

384 Acevedo P, Jiménez☐Valverde A, Lobo JM, Real R (2012) Delimiting the geographical

385 background in species distribution modelling. Journal of Biogeography 39:1383-1390.

386 https://doi.org/10.1111/j.1365-2699.2012.02713.x

387 Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution

388 models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied

389 Ecology 43:1223-1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

390 Araújo MB, Ferri☐Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL (2013) Heat

391 freezes niche evolution. Ecology Letters 16:1206-1219.

392 https://doi.org/10.1111/ele.12155

393 Arumoogum N, Schoeman MC, Ramdhani S (2019) The relative influence of abiotic and

394 biotic factors on suitable habitat of Old World fruit bats under current and future

395 climate scenarios. Mammalian Biology 98:188-200.

396 https://doi.org/10.1016/j.mambio.2019.09.006

397 Atlas of Living Australia (2020) MEGACHIROPTERA. Atlas of Living Australia. Access

398 Date 25 September 2020. https://doi.org/10.26197/5f6dc2c287312

399   Australian Government Department of Agriculture Water and the Environment (2018)

400   National Vegetation Information System (NVIS) Major Vegetation Groups.

401   Australian Government Department of Agriculture Water and the Environment. v5.1

402   Bateman BL, VanDerWal J, Johnson CN (2012) Nice weather for bettongs: using weather

403   events, not climate means, in species distribution models. Ecography 35:306-314.

404   https://doi.org/10.1111/j.1600-0587.2011.06871.x

405   Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF (2018) Present

406   and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific

407   Data 5:180214. https://doi.org/10.1038/sdata.2018.214

408   Bi DH, Dix M, Marsland SJ, O'Farrell S, Rashid HA, Uotila P, Hirst AC, Kowalczyk E,

409   Golebiewski M, Sullivan A, Yan HL, Hannah N, Franklin C, Sun ZA, Vohralik P,

410   Watterson I, Zhou XB, Fiedler R, Collier M, Ma YM, Noonan J, Stevens L, Uhe P,

411   Zhu HY, Griffies SM, Hill R, Harris C, Puri K (2013) The ACCESS coupled model:

412   description, control climate and evaluation. Australian Meteorological and

413   Oceanographic Journal 63:41-64. https://doi.org/10.22499/2.6301.004

414   Boardman WS, Baker ML, Boyd V, Crameri G, Peck GR, Reardon T, Smith IG, Caraguel

415   CG, Prowse TA (2020) Seroprevalence of three paramyxoviruses; Hendra virus,

416   Tioman virus, Cedar virus and a rhabdovirus, Australian bat lyssavirus, in a range

417   expanding fruit bat, the Grey-headed flying fox (Pteropus poliocephalus). PLoS One

418   15:e0232339. https://doi.org/10.1371/journal.pone.0232339

419   Bondarenco A, Körtner G, Geiser F (2014) Hot bats: extreme thermal tolerance in a desert

420   heat wave. Naturwissenschaften 101:679-685. https://doi.org/10.1007/s00114-014-

421   1202-2

422   Brun P, Thuiller W, Chauvier Y, Pellissier L, Wüest RO, Wang Z, Zimmermann NE (2020)

423   Model complexity affects species distribution projections under climate change.

424   Journal of Biogeography 47:130-142. https://doi.org/10.1111/jbi.13734

425   Clarke J, Whetton P, Hennessy K (2011) Providing application-specific climate projections

426   datasets: CSIROs climate futures framework. Proceedings of MODSIM, international

427   congress on modelling and simulation, modelling and simulation society of Australia

428   and New Zealand, 12-16.

429   Collins W, Bellouin N, Doutriaux-Boucher M, Gedney N, Halloran P, Hinton T, Hughes J,

430   Jones C, Joshi M, Liddicoat S (2011) Development and evaluation of an Earth-System

431   model–HadGEM2. Geoscientific Model Development 4:997-1062.

432   https://doi.org/10.5194/gmd-4-1051-2011

433   Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Bureau of

434   Meteorology (2020) Climate Change in Australia.

435   http://www.climatechangeinaustralia.gov.au/.

436   Deane-Mayer ZA, Knowles JE (2019) caretEnsemble: Ensembles of Caret Models. version

437   2.0.1. https://CRAN.R-project.org/package=caretEnsemble

438   Derham T, Mathews F (2020) Elephants as refugees. People and Nature 2:103-110.

439   https://doi.org/10.1002/pan3.10070

440   Dormann CF (2007) Promising the future? Global change projections of species distributions.

441   Basic and Applied Ecology 8:387-397. https://doi.org/10.1016/j.baae.2006.11.001

442   Dormann CF, Calabrese JM, Guillera⬚Arroita G, Matechou E, Bahn V, Bartoń K, Beale CM,

443   Ciuti S, Elith J, Gerstner K (2018) Model averaging in ecology: a review of Bayesian,

444   information⬚theoretic, and tactical approaches for predictive inference. Ecological

445   Monographs 88:485-504. https://doi.org/10.1002/ecm.1309

446   Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B,

447   Lafourcade B, Leitao PJ (2013) Collinearity: a review of methods to deal with it and a

448   simulation study evaluating their performance. Ecography 36:27-46.

449   https://doi.org/10.1111/j.1600-0587.2012.07348.x

450   Driessen M (2010) Recent sightings of flying foxes in Tasmania. The Tasmanian Naturalist

451   132:35-39.

452   Driessen M, Brereton R, Pauza M (2011) Status and conservation of bats in Tasmania.

453   Australian Zoologist 35:324-336.

454   Fick SE, Hijmans RJ (2017) WorldClim 2: new 1 km spatial resolution climate surfaces for

455   global land areas. International Journal of Climatology 37:4302-4315.

456   https://doi.org/10.1002/joc.5086

457   Fithian W, Elith J, Hastie T, Keith DA (2015) Bias correction in species distribution models:

458   pooling survey and collection data for multiple species. Methods in Ecology and

459   Evolution 6:424-438. https://doi.org/10.1111/2041-210X.12242

460   Fleming TH, Geiselman C, Kress WJ (2009) The evolution of bat pollination: a phylogenetic

461   perspective. Annals of Botany 104:1017-1043. https://doi.org/10.1093/aob/mcp197

462   Francis C, Rosell-Ambal G, Sedlock J, Ingle N, McKenzie G, Richards N (2008)

463   *Macroglossus minimus*. The IUCN Red List of Threatened Species 2008:

464   eT12594A3363390

465   https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T12594A3363390.en. Downloaded

466   on 07 April 2021.

467   Goberville E, Beaugrand G, Hautekèete NC, Piquot Y, Luczak C (2015) Uncertainties in the

468   projection of species distributions related to general circulation models. Ecology and

469   Evolution 5:1100-1116. https://doi.org/10.1002/ece3.1411

470   Graham EM, Reside AE, Atkinson I, Baird D, Hodgson L, James CS, VanDerWal JJ (2019)

471   Climate change and biodiversity in Australia: a systematic modelling approach to

472   nationwide species distributions. Australasian Journal of Environmental Management

473   26:112-123. https://doi.org/10.1080/14486563.2019.1599742

474   Greenwell BM (2017) pdp: An R Package for Constructing Partial Dependence Plots. The R

475   Journal 9:421-436. https://journal.r-project.org/archive/2017/RJ-2017-016/index.html

476   Hall LS, Richards G (2000) Flying foxes: fruit and blossom bats of Australia. UNSW Press,

477   Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling. version 3.4-5.

478   https://CRAN.R-project.org/package=raster

479   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution

480   interpolated climate surfaces for global land areas. International Journal of

481   Climatology 25:1965-1978. https://doi.org/10.1002/joc.1276

482   Hughes AC, Satasook C, Bates PJ, Bumrungsri S, Jones G (2012) The projected effects of

483   climatic and vegetation changes on the distribution and diversity of Southeast Asian

484   bats. Global Change Biology 18:1854-1865. https://doi.org/10.1111/j.1365-

485   2486.2012.02641.x

486   Hughes JM, Wilson ME, Halpin K, Hyatt AD, Plowright RK, Epstein JH, Daszak P, Field

487   HE, Wang L, Daniels PW (2007) Emerging viruses: coming in on a wrinkled wing

488   and a prayer. Clinical Infectious Diseases 44:711-717. https://doi.org/10.1086/511078

489   IPCC (2014) Climate change 2014: Synthesis Report. Contribution of Working Groups I, II

490   and III to the fifth assessment report of the Intergovernmental Panel on Climate

491   Change. IPCC, IPCC, Geneva, Switzerland.

492   IUCN (2020) The IUCN Red List of Threatened Species. https://www.iucnredlist.org.

493   Kim S, Stephen A (2018). Extreme heat wipes out almost one third of Australias spectacled

494   flying fox population. ABC News. 19 December 2018.

495   https://www.abc.net.au/news/2018-12-19/heat-wipes-out-one-third-of-flying-fox-

496   species/10632940

497   Kuhn M (2020) caret: Classification and Regression Training. version 6.0-86.

498   https://CRAN.R-project.org/package=caret

499   Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the

500   prediction of species distributions. Ecography 28:385-393.

501   https://doi.org/10.1111/j.0906-7590.2005.03957.x

502   Lunney D, Richards G, Dickman C (2008) *Pteropus poliocephalus*. The IUCN Red List of

503   Threatened Species 2008: eT18751A8554062

504   https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T18751A8554062.en. Downloaded

505   on 07 April 2021

506   Lymburner L, Tan P, McIntyre A, Thankappan M, Sixsmith J (2015) Dynamic Land Cover

507   Dataset Version 2.1. Geoscience Australia, Canberra

508   http://pid.geoscience.gov.au/dataset/ga/83868

509   MacFarlane D, Rocha R (2020) Guidelines for communicating about bats to prevent

510   persecution in the time of COVID-19. Biological Conservation 248:108650.

511   https://doi.org/10.1016/j.biocon.2020.108650

512   Martin G, Yanez-Arenas C, Chen C, Plowright RK, Webb RJ, Skerratt LF (2018) Climate

513   change could increase the geographic extent of Hendra virus spillover risk. EcoHealth

514   15:509-525. https://doi.org/10.1007/s10393-018-1322-9

515   Maxwell SL, Butt N, Maron M, McAlpine CA, Chapman S, Ullmann A, Segan DB, Watson

516   JE (2019) Conservation implications of ecological responses to extreme weather and

517   climate events. Diversity and Distributions 25:613-625.

518   https://doi.org/10.1111/ddi.12878

519   McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic

520   avian mortality events during extreme heat waves. Biology Letters 6:253-256.

521   https://doi.org/10.1098/rsbl.2009.0702

522   Morán☐Ordóñez A, Briscoe NJ, Wintle BA (2018) Modelling species responses to extreme

523   weather provides new insights into constraints on range and likely climate change

524   impacts for Australian mammals. Ecography 41:308-320.

525   https://doi.org/10.1111/ecog.02850

526   Naimi B, Araújo MB (2016) sdm: a reproducible and extensible R platform for species

527   distribution modelling. Ecography 39:368-375. https://doi.org/10.1111/ecog.01881

528   Newbold T (2018) Future effects of climate and land-use change on terrestrial vertebrate

529   community diversity under different scenarios. Proceedings of the Royal Society B:

530   Biological Sciences 285:20180792. https://doi.org/10.1098/rspb.2018.0792

531   O'shea TJ, Cryan PM, Hayman DT, Plowright RK, Streicker DG (2016) Multiple mortality

532   events in bats: a global review. Mammal Review 46:175-190.

533   https://doi.org/10.1111/mam.12064

534   Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on

535   terrestrial biota. Bulletin of the American Meteorological Society 81:443-450.

536   https://doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2

537   Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across

538   natural systems. Nature 421:37. https://doi.org/10.1038/nature01286

539   Parris KM, Hazell DL (2005) Biotic effects of climate change in urban environments: The

540   case of the grey-headed flying-fox (Pteropus poliocephalus) in Melbourne, Australia.

541   Biological Conservation 124:267-276. https://doi.org/10.1016/j.biocon.2005.01.035

542   Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009)

543   Sample selection bias and presence☐only distribution models: implications for

544   background and pseudo☐absence data. Ecological Applications 19:181-197.

545   https://doi.org/10.1890/07-2153.1

546   R Core Team (2020) R: A language and environment for statistical computing. R Foundation

547   for Statistical Computing, Vienna, Austria. version 4.0.5. https://www.R-project.org/

548   Ratnayake H, Kearney MR, Govekar P, Karoly D, Welbergen JA (2019) Forecasting wildlife

549   die☐offs from extreme heat events. Animal Conservation

550   https://doi.org/10.1111/acv.12476

551   Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in

552   relation to their biogeographic patterns. Global Change Biology 16:561-576.

553   https://doi.org/10.1111/j.1365-2486.2009.02021.x

554   Riahi K, Rao S, Krey V, Cho C, Chirkov V, Fischer G, Kindermann G, Nakicenovic N, Rafaj

555   P (2011) RCP 8.5—A scenario of comparatively high greenhouse gas emissions.

556   Climatic Change 109:33. https://doi.org/10.1007/s10584-011-0149-y

557   Roberts B, Eby P, Westcott D (2020) *Pteropus conspicillatus*. The IUCN Red List of

558   Threatened Species 2020: eT18721A22080456

559   https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T18721A22080456.en.

560   Downloaded on 07 April 2021.

561   Roberts BJ, Catterall CP, Eby P, Kanowski J (2012) Long-distance and frequent movements

562   of the flying-fox Pteropus poliocephalus: implications for management. PLoS One

563   7:e42532. https://doi.org/10.1371/journal.pone.0042532

564   Scheffers BR, Pecl G (2019) Persecuting, protecting or ignoring biodiversity under climate

565   change. Nature Climate Change 9:581-586. https://doi.org/10.1038/s41558-019-0526-

566   5

567   Schmitt S, Pouteau R, Justeau D, de Boissieu F, Birnbaum P (2017) ssdm: An r package to

568   predict distribution of species richness and composition based on stacked species

569   distribution models. Methods in Ecology and Evolution 8:1795-1803.

570   https://doi.org/10.1111/2041-210X.12841

571   Sherwin HA, Montgomery WI, Lundy MG (2013) The impact and implications of climate

572   change for bats. Mammal Review 43:171-182. https://doi.org/10.1111/j.1365-

573   2907.2012.00214.x

574   Stillman JH (2019) Heat waves, the new normal: summertime temperature extremes will

575   impact animals, ecosystems, and human communities. Physiology 34:86-100.

576   https://doi.org/10.1152/physiol.00040.2018

577   Tait J, Perotto-Baldivieso HL, McKeown A, Westcott DA (2014) Are flying-foxes coming to

578   town? Urbanisation of the spectacled flying-fox (Pteropus conspicillatus) in Australia.

579   PLoS One 9 https://doi.org/10.1371/journal.pone.0109810

580   Thapa S, Baral S, Hu Y, Huang Z, Yue Y, Dhakal M, Jnawali SR, Chettri N, Racey PA, Yu

581   W (2021) Will climate change impact distribution of bats in Nepal Himalayas? Global

582   Ecology and Conservation:e01483. https://doi.org/10.1016/j.gecco.2021.e01483

583   Thomson AM, Calvin KV, Smith SJ, Kyle GP, Volke A, Patel P, Delgado-Arias S, Bond-

584   Lamberty B, Wise MA, Clarke LE (2011) RCP4. 5: a pathway for stabilization of

585   radiative forcing by 2100. Climatic Change 109:77. https://doi.org/10.1007/s10584-

586   011-0151-4

587   Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019) Uncertainty in

588   ensembles of global biodiversity scenarios. Nature Communications 10:1-9.

589   https://doi.org/10.1002/ece3.1411

590   Tidemann CR, Nelson JE (2004) Long☐distance movements of the grey☐headed flying fox

591   (Pteropus poliocephalus). Journal of Zoology 263:141-146.

592   https://doi.org/10.1017/S0952836904004960

593   Tidemann CR, Vardon MJ, Loughland RA, Brocklehurst PJ (1999) Dry season camps of

594   flying-foxes (Pteropus spp.) in Kakadu World Heritage Area, north Australia. Journal

595   of Zoology 247:155-163. https://doi.org/10.1111/j.1469-7998.1999.tb00979.x

596   Titley MA, Butchart SH, Jones VR, Whittingham MJ, Willis SG (2021) Global inequities and

597   political borders challenge nature conservation under climate change. Proceedings of

598   the National Academy of Sciences 118 https://doi.org/10.1073/pnas.2011204118

599   van Proosdij AS, Sosef MS, Wieringa JJ, Raes N (2016) Minimum required number of

600   specimen records to develop accurate species distribution models. Ecography 39:542-

601   552. https://doi.org/10.1111/ecog.01509

602   Wallingford PD, Morelli TL, Allen JM, Beaury EM, Blumenthal DM, Bradley BA, Dukes JS,

603   Early R, Fusco EJ, Goldberg DE (2020) Adjusting the lens of invasion biology to

604   focus on the impacts of climate-driven range shifts. Nature Climate Change 10:398-

605   405. https://doi.org/10.1038/s41558-020-0768-2

606   Watanabe M, Suzuki T, O'ishi R, Komuro Y, Watanabe S, Emori S, Takemura T, Chikira M,

607   Ogura T, Sekiguchi M (2010) Improved climate simulation by MIROC5: Mean states,

608   variability, and climate sensitivity. Journal of Climate 23:6312-6335.

609   https://doi.org/10.1175/2010JCLI3679.1

610   Welbergen JA, Booth C, Martin J (2014). Killer climate: tens of thousands of flying foxes

611   dead in a day. The Conversation. 25 February 2014.

612   https://theconversation.com/killer-climate-tens-of-thousands-of-flying-foxes-dead-in-

613   a-day-23227

614   Welbergen JA, Klose SM, Markus N, Eby P (2007) Climate change and the effects of

615   temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B:

616   Biological Sciences 275:419-425. https://doi.org/10.1098/rspb.2007.1385

617   Westcott DA, McKeown A (2014) Flying foxes and drifting continents. In:Prins HH, Gordon

618   IJ (eds) Invasion Biology and Ecological Theory: Insights from a Continent in

619   Transformation. Cambridge University Press, p 138.

620   Westcott M (2010) Flying Foxes in Australia's Urban Environment. Queensland

621   Parliamentary Library,

622   Whetton P, Hennessy K, Clarke J, McInnes K, Kent D (2012) Use of representative climate

623   futures in impact and adaptation assessment. Climatic Change 115:433-442.

624   https://doi.org/10.1007/s10584-012-0471-z

625   Wisz MS, Hijmans R, Li J, Peterson AT, Graham C, Guisan A, Group NPSDW (2008)

626   Effects of sample size on the performance of species distribution models. Diversity

627   and Distributions 14:763-773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

628   Zurell D, Franklin J, König C, Bouchet PJ, Dormann CF, Elith J, Fandos G, Feng X,

629   Guillera□Arroita G, Guisan A (2020) A standard protocol for reporting species
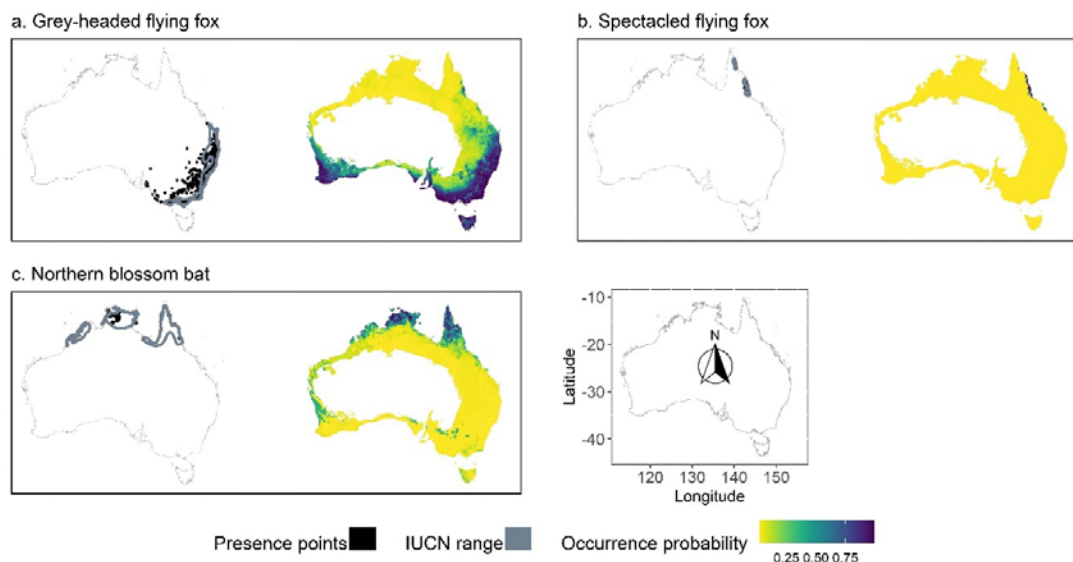
630   distribution models. Ecography https://doi.org/10.1111/ecog.04960

631   **Data Accessibility Statement**

632   The training data (csv files) and predicted models (GeoTiff files) will be made publicly

633   available via figshare with the following DOI: https://doi.org/10.6084/m9.figshare.14583282.

634   However, currently, the dataset can be shared privately on request.

635 **Table 1.** Average cross-validated AUC and TSS values attained by the best candidate model

636 for each species along with their ensemble goodness of fit AUC and TSS values. N.B. the

637 average CV and ensemble GOF metrics are not comparable to each other. The CV metrics

638 were derived from the test data during cross-validation while the GOF metrics were derived

639 using the entire training data.

Species	Predictors	Average CV AUC	Average CV TSS	Ensemble GOF AUC	Ensemble GOF TSS
Grey-headed flying fox	drt + hwave + veg + bio19 + bio8 + bio9	0.896	0.640	0.833	0.666
Spectacled flying fox	drt + hwave + veg + bio18 + bio17 + bio8	0.996	0.965	0.997	0.995
Northern blossom bat	drt + hwave + veg + bio18 + bio5 + bio9	0.941	0.660	0.964	0.929

640 *drt = drought, hwave = heatwave, veg= vegetation, bio5 = max temperature of warmest*

641 *month, bio8 = mean temperature of wettest quarter, bio9 = mean temperature of driest*

642 *quarter, bio18 = precipitation of warmest quarter, bio17 = precipitation of driest quarter,*

643 *bio19 = precipitation of coldest quarter.*

a. Grey-headed flying fox
b. Spectacled flying fox
c. Northern blossom bat

Presence points ■   IUCN range ■   Occurrence probability 0.25 0.50 0.75
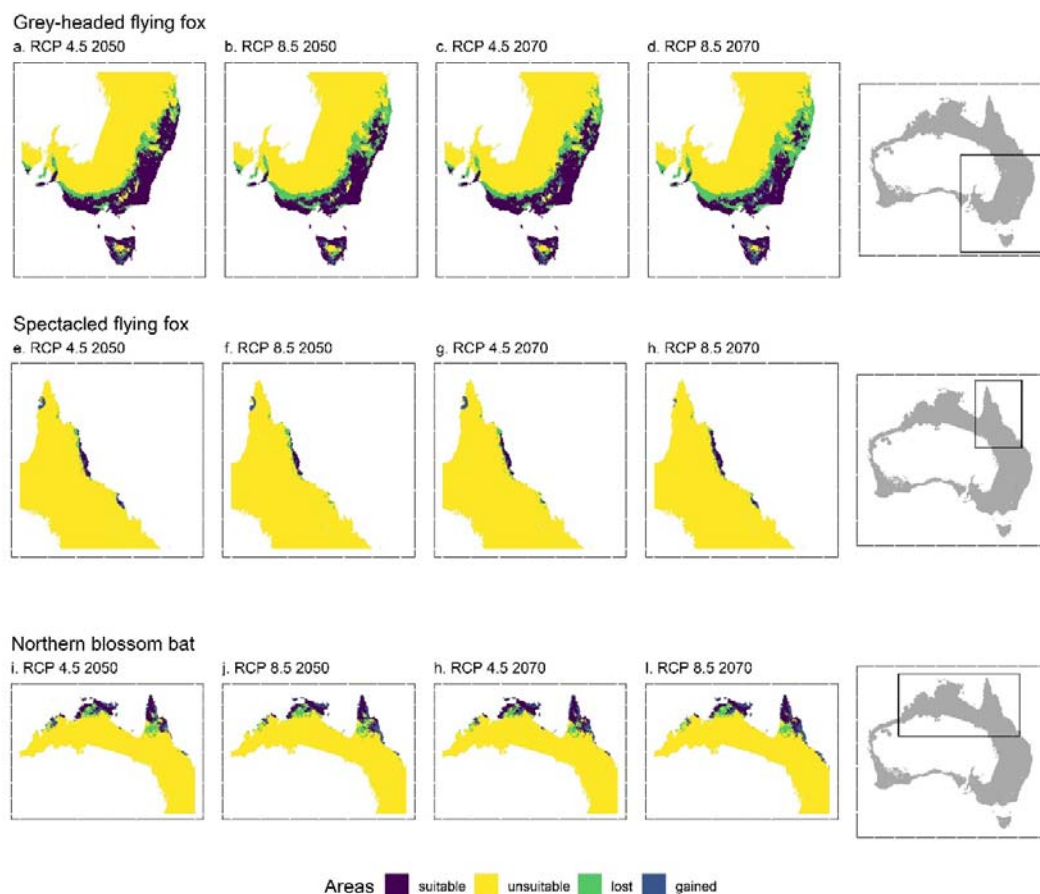
644

645   **Figure 1.** Predicted probability of occurrence of the (a) Grey-headed flying-fox, (b)

646   Spectacled flying-fox, and (c) Northern blossom bat under current climatic conditions along

647   with their presence points and IUCN range boundaries.

648
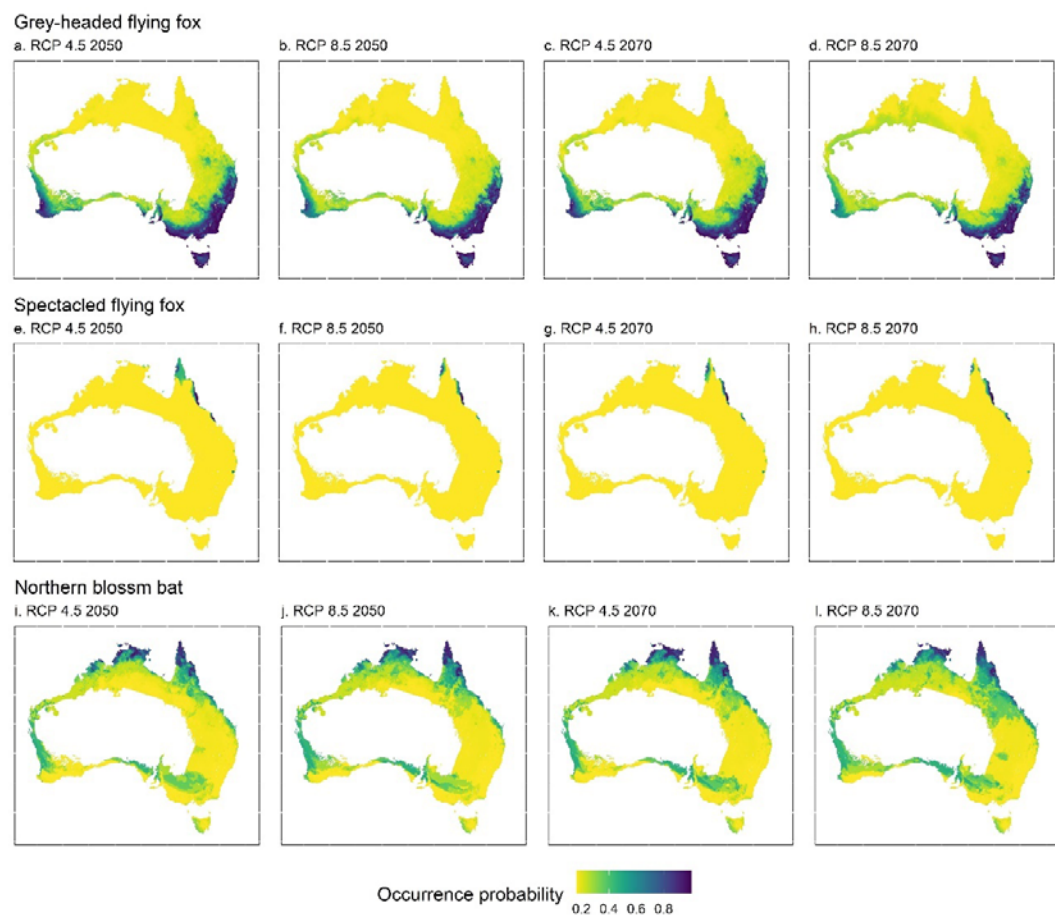
649   **Figure 2**. Predicted probability of occurrence for the Grey-headed flying-fox (a-d),

650   Spectacled flying-fox (e-h), and Northern blossom bat (i-l) under different future climatic

651   scenarios.

652

Figure 3. Predicted area suitability for the Grey-headed flying-fox (a-d), Spectacled flying-fox (e-h), and Northern blossom bat (i-l) under different future climatic scenarios.