

*Landscape functional connectivity for butterflies under different scenarios of land-use,
land-cover, and climate change in Australia*

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Declaration of competing interest

None.

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Research Data

The habitat suitability maps and functional connectivity maps are made available as GeoTiff images via Figshare (10.6084/m9.figshare.19130078).

1 **Abstract**

2 Pollinating invertebrates are vital to terrestrial ecosystems but are impacted by anthropogenic
3 habitat loss/fragmentation and climate change. Conserving and improving landscape
4 connectivity is important to offset those threats, yet its assessment for invertebrates is
5 lacking. In this study, we evaluated the functional connectivity between protected areas in
6 Australia for 59 butterfly species, under present conditions and different future scenarios (for
7 2050 and 2090) of land-use, land-cover, and climate change. Using circuit-theory analysis,
8 we found that functional connectivity under present conditions varies widely between
9 species, even when their estimated geographical ranges are similar. Under future scenarios,
10 functional connectivity is predicted to decrease overall, with negative changes worsening
11 from 2050 to 2090, although a few species are positive exceptions. We have made our results
12 available as spatial datasets to allow comparisons with taxa from other studies and can be
13 used to identify priority areas for conservation in terms of establishing ecological corridors or
14 stepping-stone habitat patches. Our study highlights the importance of considering pollinating
15 invertebrates when seeking holistic conservation and restoration of a landscape's functional
16 connectivity, underscoring the need to expand and promote protected areas to facilitate
17 functional connectivity under future scenarios of global change.

18 **Keywords**

19 Circuit theory, ecological corridors, habitat suitable models, Lepidoptera

20 **1. Introduction**

21 Landscape connectivity is defined as the extent to which the landscape facilitates the
22 movement of organisms between habitat patches. It can be structural or functional; the former
23 is dependent on only the landscape structure, while the latter (which is of focus in this study)
24 also considers species attributes such as habitat preference and dispersal ability (Rudnick et
25 al. 2012; Costanza and Terando 2019). Habitat loss and fragmentation increase barriers
26 between suitable habitats reducing gene flow and the ability of a species to track climate
27 change. Maintaining and restoring landscape connectivity is considered as an important
28 adaptation strategy to reduce the impact of habitat loss and fragmentation and climate change
29 and thereby better conserve biodiversity (Rudnick et al. 2012; Costanza and Terando 2019;
30 Littlefield et al. 2019).

31 Studies on habitat connectivity (i.e., the degree of functional connectivity between patches of
32 preferred or obligate habitat for individual species) are typically biased towards mammals
33 and birds (Correa Ayram et al. 2016; Dickson et al. 2019). This leaves a gap in the literature
34 for invertebrates—particularly pollinating invertebrates—although there are exceptions (e.g.
35 Filz et al. 2013; Chen 2017; Kirk et al. 2018; Miranda et al. 2021). This gap needs to be
36 filled, as habitat connectivity is important for sustaining pollinator abundance, diversity, and
37 dispersal (Potts et al. 2016). Indeed preserving habitat connectivity is an important strategy
38 for conserving insects (Samways et al. 2020) and its loss can have a negative impact on
39 pollination (Mitchell et al. 2013).

40 Butterflies make for an ideal functional-connectivity case study because they are a major
41 pollinating taxon thought to be able to transfer pollen over larger distances than other insects
42 (Winfree et al. 2011) and are demonstrably impacted by habitat loss/fragmentation and
43 climate change (Miao et al. 2020; Warren et al. 2021). In some regions, available protected

44 areas are inadequate for butterfly conservation (Chowdhury et al. 2021a) while in other cases,
45 the effectiveness of protected areas for butterflies is predicted to decrease under climate
46 change (Cheng and Bonebrake 2017). Expanding and improving the connectivity of protected
47 areas is part of the Aichi Biodiversity Targets (Target 11; Convention on Biological Diversity
48 2022). Thus, maintaining and promoting ecological corridors or stepping-stone habitats is
49 critical to facilitate species movement between metapopulations to prevent inbreeding and
50 promote recolonisation after extirpation events (Sands 2018), as well as to facilitate
51 movement in response to climate change (Stewart et al. 2019; Malakoutikhah et al. 2020).

52 The aim of this study is to assess the landscape-scale functional connectivity for butterflies
53 between protected areas in Australia, under both present conditions and different future
54 scenarios of land-use, land-cover and climate change (for 2050 and 2090). We assessed the
55 connectivity for 59 species of butterflies using the *Circuitscape* Julia package (Anantharaman
56 et al. 2020) which is based on circuit theory (McRae et al. 2008). *Circuitscape* uses circuit
57 theory to predict patterns of movement or dispersal of organisms or genes (McRae et al.
58 2008) and has been used for studying landscape population genetics and identifying animal
59 movement corridors (Dickson et al. 2019). Circuit theory operates on a continuous layer and
60 considers multiple pathways for movements, making it more flexible than other, simpler
61 methods like the least-cost pathway (McRae et al. 2008). We then considered the
62 conservation implications of our findings for habitat prioritisation.

63

64 **2. Materials and Methods**

65 *2.1 Butterfly species*

66 Occurrence (presence) data were from the Atlas of Living Australia occurrence downloaded
67 at <https://doi.org/10.26197/ala.9028e7dc-2566-44de-8999-dbb36c6685a9> Accessed 15
68 February 2021. Records were limited to those from 1960 onwards and classified as ‘human
69 observation’. Duplicate records based on latitude and longitude were removed. We used
70 spatial thinning to reduce spatial autocorrelation by removing records closer than a minimum
71 nearest neighbour distance (NMD) using the R package *spThin* (Aiello-Lammens et al. 2015).
72 We followed the method by Amin et al. (2021) to find the optimal NMD for each species
73 separately – adjusting it based on the human activity index. To achieve this, firstly, we
74 stratified Australia into low, medium and high human activity grids of resolution 25 km²
75 using Global Human-Footprint data (Venter et al. 2018). Secondly, we removed all records
76 (i.e., of all species combined) closer than 1.25 km to ensure that data in low-density grids
77 were relatively uncorrelated. Then, for each species, we estimate the threshold number of re-
78 samples to be retained per grid (h) using: $h = n_i/N_i$ where n_i represents the number of samples
79 in low-activity grids and N_i is the number of low-activity grids. The threshold values were
80 then applied to calculate the maximum number of re-samples to be retained from medium and
81 high-density grids, using the formula: $n_{jk} = h \times N_{jk}$, where n is the maximum number of re-
82 samples from medium j or high k density grids, and N is the number of medium j or high
83 grids k . This was repeated 20 times per sampling run and tuned the NMD for high- and
84 medium-activity grids to achieve the maximum number of re-samples (n_{jk}) for each species.

85 To enable robust model training and validation, we selected only species with at least 100
86 unique occurrence records (after removing duplicates and accounting for spatial
87 autocorrelation) for high model performance and estimation of geographical ranges. An
88 exception to this rule was made for the Ptunarra Brown Butterfly (*Oreixencia ptunarra*
89 Couchman 1953) which had 96 records as it is a threatened species (Geyle et al. 2021). We
90 pooled all subspecies into their respective species as this enabled each species to have an

91 adequate number of occurrence records. Consequently, we modelled 59 species in this study,
92 belonging to the Nymphalidae, Lycaenidae, Hesperidae, Papilionidae families (Supplemental
93 Table A1).

94 *2.2 Habitat suitability models*

95 In this study, we used habitat-suitability maps as the ‘resistance layer’ which represents the
96 degree to which the landscape facilitates or blocks the movement of an individual across a
97 given cell. Here, high suitability indicates low resistance (and therefore, a high probability of
98 movement). Habitat suitability models are commonly used to estimate resistance in
99 connectivity models (Correa Ayram et al. 2016), and this approach has the advantage of also
100 providing an opportunity to assess the potential impact of climate change on functional
101 connectivity (Ashrafzadeh et al. 2019; Bonnin et al. 2020; Malakoutikhah et al. 2020).

102 To model habitat suitability, we selected all 19 bioclimatic variables (version 2.1;
103 <https://www.worldclim.org>; Fick and Hijmans 2017), elevation (<https://www.worldclim.org>),
104 and land-use and land-cover change (LULCC; Li et al. 2017) as predictors. The LULCC
105 variable was resampled to match the resolution of the bioclimatic and elevation variables
106 (0.05°, or ~5 km at Australian latitudes) using the *raster* R package (Hijmans 2020). We then
107 reduced the number of predictors by removing highly correlated predictors using a threshold
108 value of 0.7 (Dormann et al. 2013) and implemented using the *findCorrelation* function in
109 *caret* R package (Kuhn 2021). If two variables were highly correlated, then the variable with
110 the largest mean absolute correlation was removed. All non-correlated predictors were used
111 for model fitting for each species (Supplementary Table A1).

112 The study area for each species was constrained using its estimated kernel geographical
113 range, which was implemented using the *adehabitatHR* R package (Calenge 2006). We
114 assumed that a species can disperse within the entirety of its geographical range.

115 Pseudo-absences were generated using a random sampling method, with the presence to
116 pseudo-absence ratio set to unity. We used k-fold cross-validation ($k=10$) for algorithm
117 optimisation and implemented using the *caret* R package (Kuhn 2021). The algorithms used
118 in the study include random forest, artificial neural network, k-nearest neighbour, flexible
119 discriminant analysis, and naïve Bayes, as they have different operating mechanisms and so
120 capture a diversity of machine-learning approaches.

121 Random forest is decisions trees based on bagging (Breiman 2001). Artificial neural network
122 consists of a network of neurons that are considered as the processing units in a strictly feed-
123 forward neural network (Sazli 2006). k-nearest neighbour works under the assumption that
124 similar things exist in proximity (in parameter hyperspace) and thus classifies data most
125 common among its neighbours (Cover and Hart 1967). Flexible discriminant analysis uses
126 multivariate adaptive regression splines to separate the data (Hastie et al. 1994), while naïve
127 Bayes is based on conditional probability (Ren et al. 2009).

128 Habitat-suitability models were fitted using the trained algorithms, and then ensembled. An
129 ensemble algorithm averages the prediction of structurally different algorithms and has the
130 potential to overcome uncertainty in model selection and improve prediction accuracy by
131 reducing variance and bias (Dormann et al. 2018). As such, we averaged the algorithms using
132 an unweighted method and assessed the goodness of fit using AUC and TSS (Allouche et al.
133 2006).

134 To account for the influence of global climate models (GCMs) we selected CanESM5 and
135 MIROC6, which have been used in previous studies in Australia (e.g., Briscoe et al. 2016;
136 Ofori et al. 2017; Morán-Ordóñez et al. 2018) under Shared Socio-economic Pathways
137 (SSP) 7.0, a high-emission scenario (IPCC 2021). For the LULCC variable, we selected A1
138 (low population growth, sprawling urban expansion, very high economic growth, rapid

139 technological innovation, strong biofuels demand including cellulose-based ethanol) and B1
140 (low population growth, compact urban expansion, high economic growth, medium
141 technological innovation, low overall energy use, lower demand for biofuels) scenarios which
142 are both oriented globally (Li et al. 2017). Future predictions were made for each species per
143 algorithm per year per climate model per LULCC scenario, and then ensembled (unweighted)
144 per year (2050 and 2090).

145 *2.3 Functional connectivity models*

146 Functional connectivity was assessed using the *Circuitscape* package in the Julia
147 Programming Language (Anantharaman et al. 2020). *Circuitscape* calculates connectivity
148 between focal nodes (habitat patches or populations) across a resistance layer (represents the
149 degree to which the landscape impedes the movement of an individual across a given cell)
150 and in analogy to an integrated circuit board in electronics, then calculates the effective
151 resistance and ‘current flow’ which in the ecological interpretation is a measure of net
152 movement probability (McRae et al. 2008). The modelling of functional connectivity results
153 in maps with cumulative current, where the intensity of current is a proxy for a species’
154 movement at each pixel (Grafius et al. 2017).

155 In this study, we used the centroids of protected areas as focal nodes (Mukherjee et al. 2021);
156 for this purpose, we only selected protected areas with an average habitat suitability of ≥ 0.7
157 as this represented a high threshold of suitability. We identified focal nodes for each species
158 individually, under present climate conditions and future climate-change scenarios (for 2050
159 and 2090).

160 The resistance layer in our study of butterflies is equal to the sum of the habitat suitability
161 model and Global Human Footprint data (Venter et al. 2018). The Global Human Footprint is
162 a measure of human impact (Venter et al. 2018), where cells with high impact are associated

163 with high resistance, likely to be a function of dispersal limitation rather than habitat
164 suitability, as urban and agricultural areas can reduce the ability of butterflies to move across
165 landscapes and infrastructure such as roads results in significant mortality of butterflies
166 (Chowdhury et al. 2021b). The predicted habitat-suitability data ranges from 0.0 to 1.0 (low
167 to high resistance), while the Global Human Footprint data ranges from 0.0 to 100.0 (high to
168 low). To match the scale and direction of these two data sets, we transformed the habitat
169 suitability data by subtracting the data from 1 and multiplying it by 100. The transformed
170 habitat suitability data was added to the Global Human Footprint data and then rounded up to
171 the nearest integer, because *Circuitscape* does not accept non-integer values. Due to the
172 unavailability of future Global Human Footprint data, we were forced to assume that this data
173 is constant under present conditions and future scenarios. The final resistance layer scales
174 from 0 to 200 (lowest to highest possible resistance). Resistance layers were created for each
175 species under present climate conditions and future climate scenarios (for 2050 and 2090).

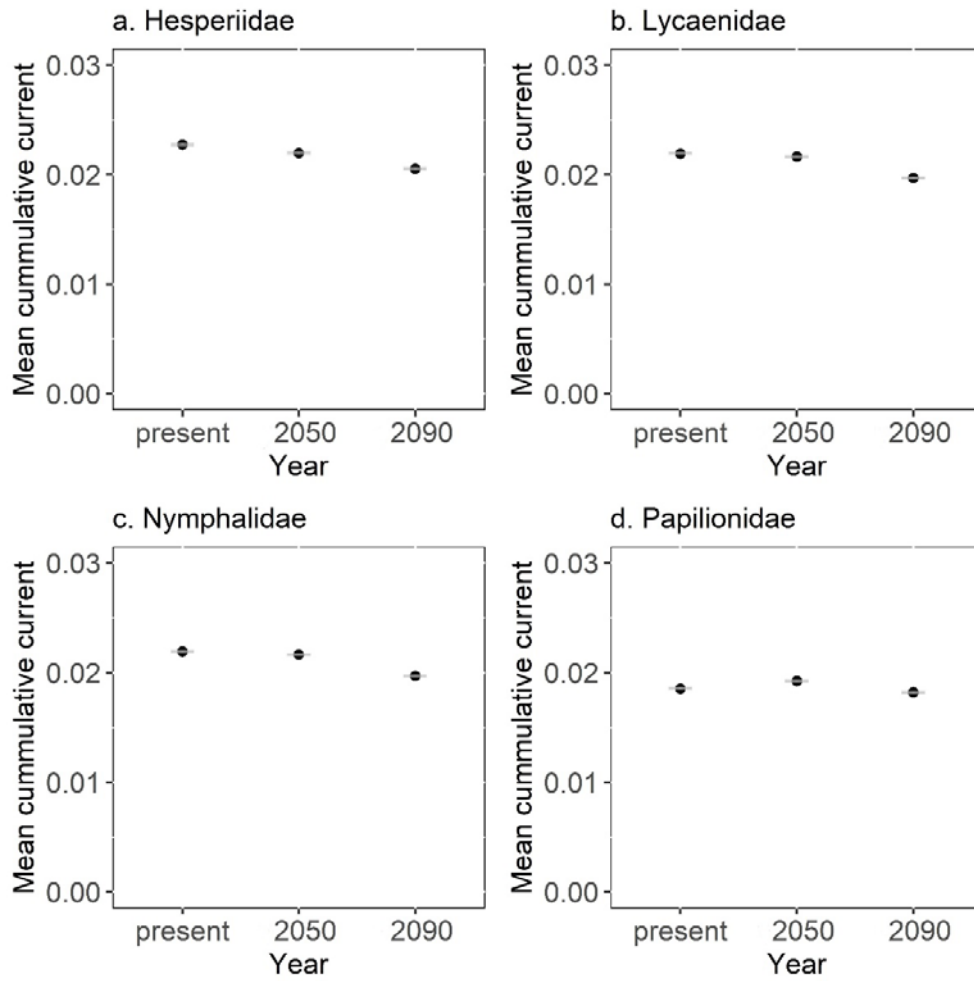
176 We predicted the functional connectivity for each species under present conditions and then
177 calculated their goodness of fit (AUC) to assess model accuracy (Jackson et al. 2016). We
178 also calculated the mean cumulative current (with standard error) of the connectivity models.
179 If a pixel facilitates connectivity, then the presence points should on average have higher
180 values than pseudo-absences (Grafius et al. 2017; Rodrigues et al. 2021). We then predicted
181 the functional connectivity for each species under future scenarios (for 2050 and 2090). And
182 assessed the difference in functional connectivity between present conditions and future
183 scenarios (i.e., future minus present functional connectivity model) as well.

184

185 **3. Results**

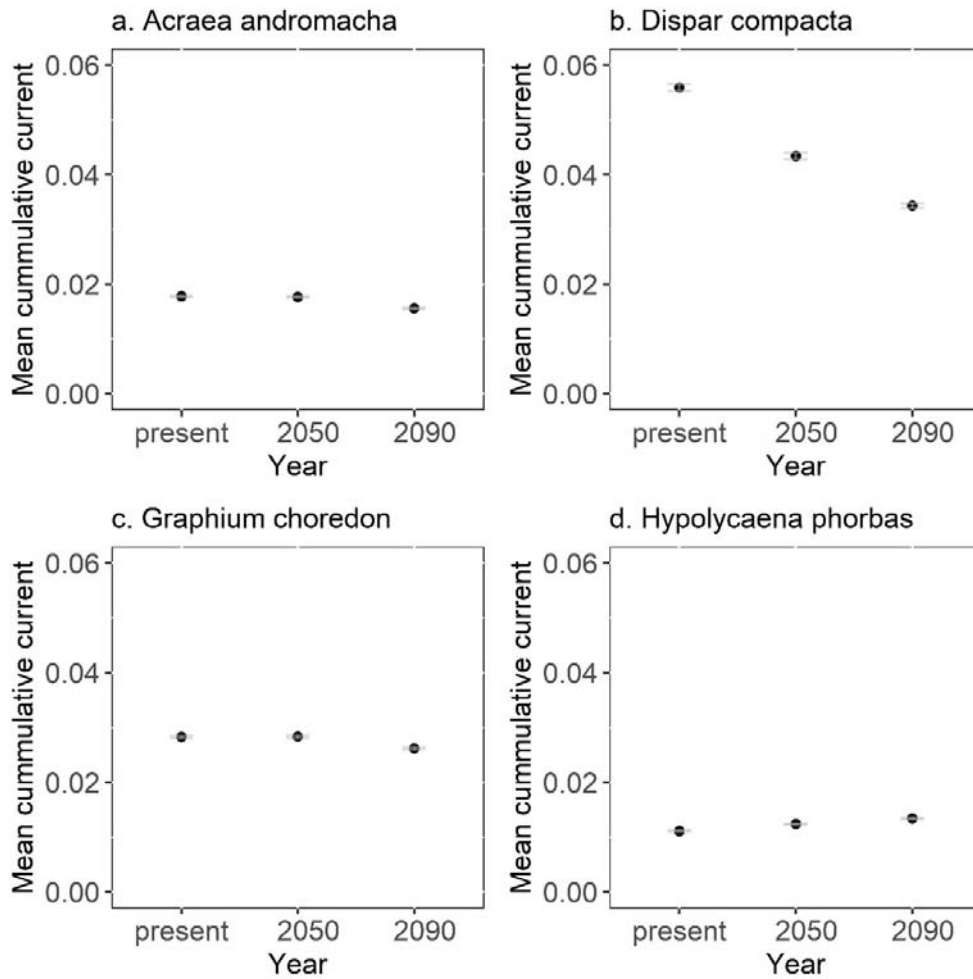
186 The habitat suitability models for all 59 Australian butterfly species with sufficient data
187 achieved high goodness of fit for both AUC and TSS scores. The highest and lowest AUC
188 scores were 0.99 and 0.94 respectively, while the highest and lowest TSS scores were 0.92
189 and 0.65 respectively (Supplemental Table A1). The connectivity models also achieved high-
190 to-moderate goodness of fit, with AUC scores ranging between 0.94 and 0.68
191 (Supplementary Table A1). The mean cumulative current of the presence points was higher
192 than that of the pseudo-absences for functional connectivity models of all species
193 (Supplementary Fig. A1-2).

194 The circuit-theory results (a proxy for functional connectivity) of all the families except for
195 Papilionidae predicted similar future trends, with mean cumulative current expected to
196 decrease through to 2090 (Fig. 1). However, the results for individual species provided a
197 more nuanced perspective than looking at families and exhibited considerably more variation.
198 For example, *Dispar compacta* (Hesperiidae) has a higher mean cumulative current than
199 *Hypolycaena phorbas* (Lycaenidae) with current predicted to decrease for the former and
200 increase for the latter (Fig. 2b, d), whereas for *Acraea andromacha* (Nymphalidae) and
201 *Graphium choredon* (Papilionidae), future scenarios show similar results to present-day
202 conditions (Fig. 2a, c).



203

204 **Fig 1.** Mean cumulative current with standard error of the families (a) Hesperiiidae (b)
205 Lycaenidae, (c) Nymphalidae, and (d) Papilionidae under present conditions and future
206 scenarios of climate change (for the year 2050 and 2090).

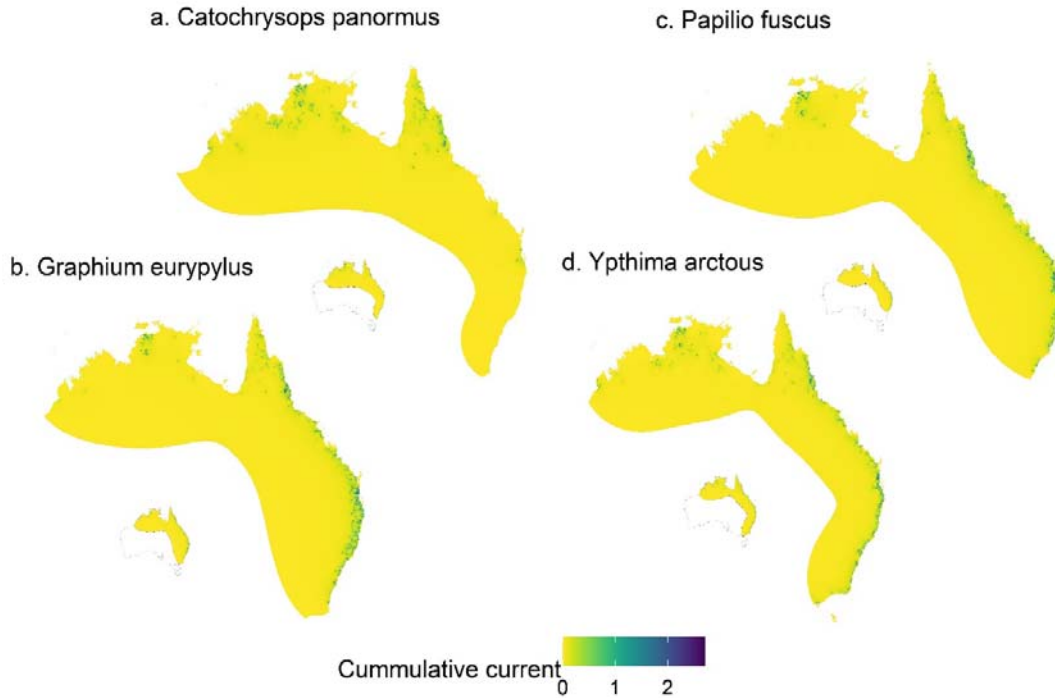


207

208 **Fig 2.** Mean cumulative current with standard error of the species (a) *Acraea andromacha* (b)
209 *Dispar compacta*, (c) *Graphium choredon*, and (d) *Hypolycaena phorbis* under present
210 conditions and future scenarios (the year 2050 and 2090).

211

212 Under present conditions, functional connectivity is modelled to vary between species and
213 regionally, including those with similar geographical ranges. For example, *Catochrysops*
214 *panormus* has higher connectivity along the northern part of Australia than *Graphium*
215 *eury pylus*, *Papilio fuscus*, and *Ypthima arctous* (Fig. 3), while *Graphium eury pylus* and
216 *Ypthima arctous* have higher connectivity along the eastern coast than the other species (Fig
217 3), although those species are found across a similar geographic range.



218

219 **Fig 3.** Functional connectivity of the species (a) *Catochrysops panormus* (b) *Graphium*
220 *eurypylus*, (c) *Papilio fuscus*, and (d) *Ypthima arctous* under present-day conditions.

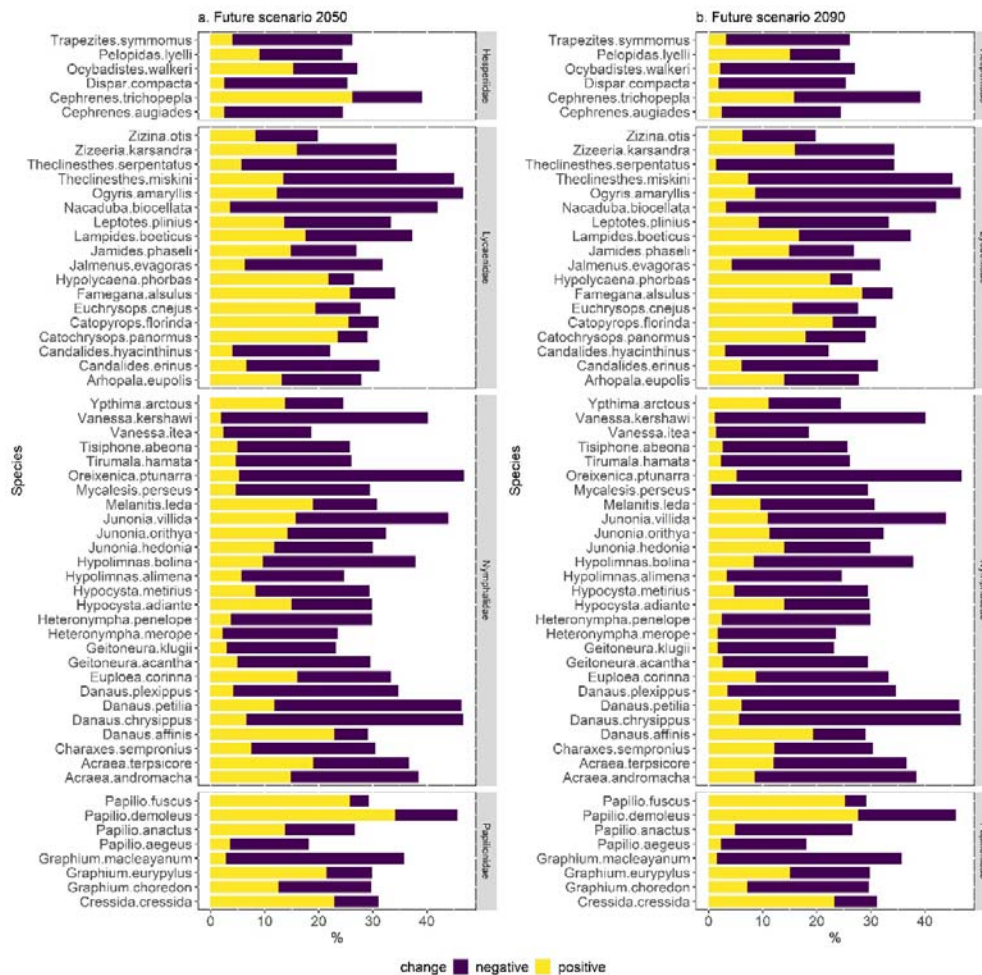
221

222 Most species (43 out of 59) showed consistent, ongoing declines in functional connectivity
223 between the present and 2090 (Fig. 4). For *Arhopala eupolis*, *Candalides erinus*, *Cephrenes*
224 *augiades*, *Jamides phaseli*, *Nacaduba biocellata*, *Oreixenica ptunarra*, *Papilio fuscus*,
225 *Trapezites symmomus*, and *Vanessa kershawi* (9 out of the 59 species) the percentage of
226 change between future scenarios 2050 and 2090 are similar (Fig 4). While for *Charaxes*
227 *sempronius*, *Cressida cressida*, *Famegana alsulus*, *Hypolycaena phorbis*, *Junonia hedonia*,
228 *Pelopidas lyelli*, and *Zizeeria karsandra* (7 out of the 59 species) the percentage of positive
229 changes is higher in the year 2090 than in 2050 (Fig 4).

230

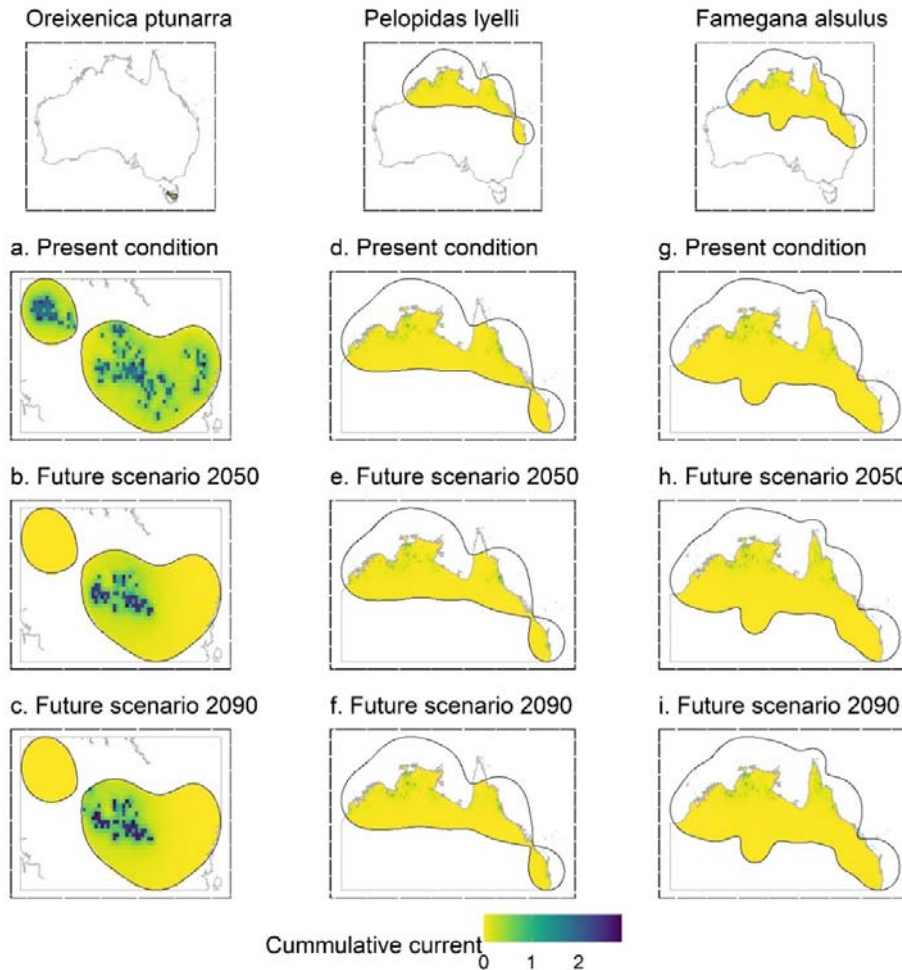
231 Although the percentage of change between future scenarios 2050 and 2090 are similar, for
the *Oreixenica ptunarra* (Fig. 4) functional connectivity is still predicted to decrease,

232 particularly along the north-west and eastern parts of its range (Fig. 5a-c). And while the
 233 percentage of positive changes is higher in the year 2090 than 2050 for *Pelopidas lyelli* and
 234 *Famegana alsulus* (Fig 4) functional connectivity is predicted to increase along the southern
 235 part of the range for *Pelopidas lyelli* (Fig. 5d-f) and along the north-eastern part of the range
 236 for *Famegana alsulus* (Fig. 5g-i)



237

238 **Fig 4.** Percentage of negative and positive changes in functional connectivity for each
 239 Australian butterfly species, grouped by family, under future scenarios (a) 2050 and (b) 2090.

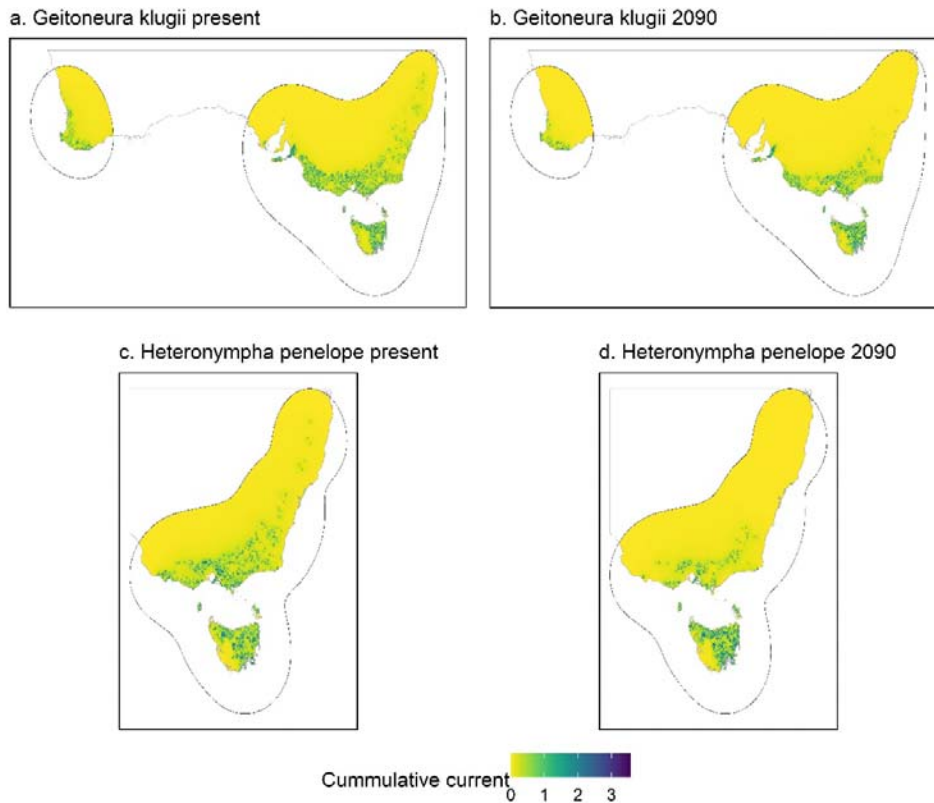


240

241 **Fig 5.** Functional connectivity of the species (a-c) *Oreixenica ptunarra*, (d-f) *Pelopidas lyelli*,
242 and (g-i) *Famegana alsulus* under present conditions and future scenarios (for 2050 and
243 2090).

244

245 Changes in functional connectivity were predicted to occur both along the periphery of a
246 species' geographical range and within the core. For example, functional connectivity was
247 predicted to be lost along the north-east range for *Geitoneura klugii* and *Heteronympha*
248 *Penelope* (Fig. 6) as well as within the core of their ranges. In some cases, functional
249 connectivity is also predicted to increase along the edges, for example, there is an increase
250 along the south-west of the island of Tasmania for the *Geitoneura klugii* (Fig. 6a, b).



251

252 **Fig 6.** Functional connectivity of *Geitoneura klugii* (a-b) and *Heteronympha penelope* (c-d)
253 under present conditions and future scenarios.

254

255 **4. Discussion**

256 Butterflies are an ecologically important and conspicuous pollinating taxon that is threatened
257 by habitat loss/fragmentation and climate change (Miao et al. 2020; Warren et al. 2021).

258 These threats can be mitigated by conserving and promoting functional connectivity, making
259 it crucial that ecologists seek to identify such areas. Overall, our analysis predicts that

260 functional connectivity will show an overall decrease, with most butterfly species

261 experiencing a higher percentage of negative changes than positive; a trend that worsens over

262 time. Below we highlight how modelling can assist in the decision making of where

263 ecological corridors and stepping-stone habitats should be prioritised.

264 Under present conditions, the mean cumulative current is overall predicted to be higher along
265 areas with core habitats or focal nodes (i.e., areas with high habitat suitability); a finding
266 common to studies of other taxa such as African elephants (Roever et al. 2013), birds
267 (Grafius et al. 2017), and ungulates (Malakoutikhah et al. 2020). The differences and
268 similarities in functional connectivity between butterfly species with similar (estimated)
269 ranges can be attributed, in large part, to their habitat preferences. For example, *C. panormus*
270 (functional connectivity predicted to decrease; Fig 4) occur in open eucalyptus forest and
271 savannah woodland, whereas *G. eurypylus* (functional connectivity predicted to decrease; Fig
272 4) occur in monsoon forest, rainforest, and even urban gardens (Braby 2000). As another
273 relevant contrast of species with similar-sized geographic ranges but different responses are,
274 *P. fuscus*, (functional connectivity predicted to remain similar between 2050 and 2090; Fig 4)
275 being found in coastal and subcoastal lowlands rainforest and monsoon forest, compared to *Y.*
276 *arctous* (functional connectivity predicted to decrease; Fig 4), which prefers coastal and
277 subcoastal woodlands and open forest (Braby 2000).

278 Overall, we predicted the functional connectivity of most butterfly species in Australia to
279 decrease over the coming decades, albeit with a few exceptions. Our predictions are similar to
280 studies that predicted several non-butterfly taxa such as the Sichuan snub-nosed monkey
281 (Zhang et al. 2019b), ungulates (Malakoutikhah et al. 2020; Liang et al. 2021), and the
282 Himalayan brown bear (Mukherjee et al. 2021) to experience a future decrease in functional
283 connectivity due to climate change in different parts of the world. To our knowledge, this is
284 the first attempt to predict the combined impacts of land-use, land-cover, and climate change
285 on the functional connectivity of butterflies.

286 The mean cumulative circuit-theory ‘current’ is overall predicted to be highest along areas
287 with the best habitat suitability for a given species. The predicted decrease in functional
288 connectivity for most species is expected because climate change is predicted to change the

289 geographic distributions of butterflies (Adhikari et al. 2020; Minachilis et al. 2021). Overall,
290 most of the changes are predicted along the edges of a species range, because populations
291 along boundaries are generally inhabiting the limits of their physiological tolerances
292 compared to those at the core, leaving them more vulnerable to climate change (Parmesan et
293 al. 2000). These changes could also be due to land-use and land-cover change which is
294 observed (Zhang et al. 2019a; Wang et al. 2020) and predicted (Li et al. 2017) to result in loss
295 of forest areas which could have negative impacts on species depending on such habitats.
296 Overall land-use and land-cover change have a negative impact on biodiversity in Australia
297 including on butterflies (Thackway 2018; Davidson et al. 2021; Kutt et al. 2021).

298 Given the continental scale of the study area and the number of species assessed, there were a
299 few limitations to the study. Spatial scale can influence functional connectivity models
300 (Laliberté and St-Laurent 2020) and while 1-km spatial resolution predictors are available,
301 the extent of the study area and the high computational requirements forced us to use a
302 coarser resolution of 5 km. The accuracy of the habitat suitability models can be influenced
303 by several factors, including the temporal equilibrium (or lack thereof) between data points
304 (species observations) and the geophysical and landscape predictors, as well as the interaction
305 between the spatial scale of the predictors and attributes of the species (Dormann 2007).

306 Validating functional connectivity models is a challenging process (Laliberté and St-Laurent
307 2020), with suggested methods including field observations by scientists or automated field
308 recorders (e.g., camera traps, acoustic recorders), along with accurate GPS data (Grafius et al.
309 2017; Finch et al. 2020; Laliberté and St-Laurent 2020). However, in this study, we used
310 citizen science data to build and validate the models, because of the scale of the study area
311 and the number of species studied, which has the advantage of volume, but the constraint of a
312 lower-level of precision and quality control.

313

314 **5. Conclusion**

315 Butterflies are an important pollinating group, but the functional connectivity for several
316 species are predicted to decrease across Australia in the coming decade due to the combined
317 impacts of land-use, land-cover and climate change. Conservation efforts are being made to
318 improve ecological corridors and stepping-stone habitat-restoration programs to promote
319 functional connectivity, in some cases these efforts include invertebrates such as bees (e.g.,
320 Miranda et al. 2021) in other cases the focus is only on vertebrate taxa (e.g., Jones et al.
321 2021). We advocate conservation efforts should include butterflies and other pollinating taxa
322 as well. The availability of our results as a spatial dataset, along with analogous findings from
323 other taxa, will assist in identifying priority conservation areas. Future studies on butterflies
324 should consider (1) collecting dispersal data, to build better connectivity models given that
325 radio telemetry for butterflies is now becoming a logistically viable option (Wang et al.
326 2019), (2) improving the resistance layer by including spatial data that contains food plants
327 that caterpillars feed upon and butterflies pollinate (Kass et al. 2020), and (3) focussing on
328 species most threatened (Geyle et al. 2021), to develop more targeted, species-specific
329 conservation efforts.

330

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