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

Vishesh L. Diengdoh¹, e: vishesh.diengdoh@utas.edu.au, ORCID: <https://orcid.org/0000-0002-0797-9261>

Stefania Onde¹ - e: stefania.ondei@utas.edu.au

Rahil J. Amin¹ - e: RahilJasminkumar.Amin@utas.edu.au

Mark Hunt^{1,3} - e: M.Hunt@utas.edu.au

Barry W. Brook^{1,2} - e: barry.brook@utas.edu.au

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

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

³ARC Industrial Transformation Training Centre for Forest Value, Australia

Corresponding Author: Vishesh L. Diengdoh

Authors contribution

Conceptualisation: VLD; Methodology: VLD, BWB, SO, RJA; Analysis: VLD, RJA;
Writing (original draft): VLD; Writing (review) VLD, BWB, SO, RJA, MH; Supervision:
BWB, SO, MH; Funding: BWB.

Declaration of competing interest

None.

Acknowledgements

This work was supported by the Australian Research Council [grant number FL160100101].

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

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

2.2 Habitat suitability models

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

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

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

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

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

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

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

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

2.3 Functional connectivity models

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

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

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

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

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

3. Results

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

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

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

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

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

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

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

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,

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

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

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

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

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

4. Discussion

Butterflies are an ecologically important and conspicuous pollinating taxon that is threatened by habitat loss/fragmentation and climate change (Miao et al. 2020; Warren et al. 2021). These threats can be mitigated by conserving and promoting functional connectivity, making it crucial that ecologists seek to identify such areas. Overall, our analysis predicts that functional connectivity will show an overall decrease, with most butterfly species experiencing a higher percentage of negative changes than positive; a trend that worsens over time. Below we highlight how modelling can assist in the decision making of where ecological corridors and stepping-stone habitats should be prioritised.

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

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

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

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

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

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

5. Conclusion

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

References

Adhikari P, Jeon J-Y, Kim HW, Oh H-S, Adhikari P, Seo C (2020) Northward Range Expansion of Southern Butterflies According to Climate Change in South Korea. *Journal of Climate* 11(6-1):643-656 <http://dx.doi.org/10.15531/KSCCR.2020.11.6.643>

335 Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an
336 R package for spatial thinning of species occurrence records for use in ecological niche
337 models. *Ecography* 38(5):541-545 <https://doi.org/10.1111/ecog.01132>

338 Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution
339 models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*
340 43(6):1223-1232 <https://doi.org/10.1111/j.1365-2664.2006.01214.x>

341 Amin RJ, Buettel JC, Fielding MW, Vaughan PM, Brook BW (2021) Hot, unpredictable
342 weather interacts with land use to restrict the distribution of the Yellow-tailed Black-
343 Cockatoo. *Emu - Austral Ornithology*:1-10 <https://doi.org/10.1080/01584197.2021.1952083>

344 Anantharaman R, Hall K, Shah V, Edelman A (2020) Circuitscape in Julia: High
345 Performance Connectivity Modelling to Support Conservation Decisions. *Proceedings of the*
346 *JuliaCon Conferences* 1:1 <https://doi.org/10.21105/jcon.00058>

347 Ashrafzadeh MR, Naghipour AA, Haidarian M, Kusza S, Pilliod DS (2019) Effects of
348 climate change on habitat and connectivity for populations of a vulnerable, endemic
349 salamander in Iran. *Global Ecology and Conservation* 19:e00637
350 <https://doi.org/10.1016/j.gecco.2019.e00637>

351 Bonnin N, Stewart FA, Wich SA, Pintea L, Jantz SM, Dickson R, Bellis J, Chitayat A,
352 Ingram R, Moore RJ (2020) Modelling landscape connectivity change for chimpanzee
353 conservation in Tanzania. *Biological Conservation* 252:108816
354 <https://doi.org/10.1016/j.biocon.2020.108816>

355 Braby MF (2000) *Butterflies of Australia: their identification, biology and distribution*.
356 CSIRO publishing

357 Breiman L (2001) Random forests. Machine learning 45(1):5-32
358 <https://doi.org/10.1023/A:1010933404324>

359 Briscoe NJ, Kearney MR, Taylor CA, Wintle BA (2016) Unpacking the mechanisms
360 captured by a correlative species distribution model to improve predictions of climate refugia.
361 Global Change Biology 22(7):2425-2439 <https://doi.org/10.1111/gcb.13280>

362 Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of
363 space and habitat use by animals. Ecological Modelling 197(3-4):516-519
364 <https://doi.org/10.1016/j.ecolmodel.2006.03.017>

365 Chen N (2017) Assessing Landscape Effects on Genetics and Dispersal of the Rocky
366 Mountain Apollo Butterfly *Parnassius smintheus* using a Resistance Mapping Approach. The
367 University of Western Ontario <https://ir.lib.uwo.ca/etd/5058>

368 Cheng W, Bonebrake TC (2017) Conservation effectiveness of protected areas for Hong
369 Kong butterflies declines under climate change. Journal of Insect Conservation 21(4):599-
370 606 <https://doi.org/10.1007/s10841-017-9998-7>

371 Chowdhury S, Alam S, Chowdhury SU, Rokonuzzaman M, Shahriar SA, Shome AR, Fuller
372 RA (2021a) Butterflies are weakly protected in a mega-populated country, Bangladesh.
373 Global Ecology and Conservation 26:e01484 <https://doi.org/10.1016/j.gecco.2021.e01484>

374 Chowdhury S, Fuller RA, Dingle H, Chapman JW, Zalucki MP (2021b) Migration in
375 butterflies: a global overview. Biological Reviews <https://doi.org/10.1111/brv.12714>

376 Convention on Biological Diversity (2022) Aichi Biodiversity Target. Accessed 04 February
377 2022 <https://www.cbd.int/aichi-targets/>

- 378 Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in
379 biodiversity conservation: A review of recent studies and applications. Progress in Physical
380 Geography 40(1):7-37 <https://doi.org/10.1177/0309133315598713>
- 381 Costanza JK, Terando AJ (2019) Landscape connectivity planning for adaptation to future
382 climate and land-use change. Current Landscape Ecology Reports 4(1):1-13
383 <https://doi.org/10.1007/s40823-019-0035-2>
- 384 Cover TM, Hart PE (1967) Nearest Neighbor Pattern Classification. IEEE Transactions on
385 Information Theory 13(1):21-27 <https://doi.org/10.1109/Tit.1967.1053964>
- 386 Davidson NJ, Bailey TG, Burgess S (2021) Restoring the Midlands of Tasmania: an
387 introduction. Ecological Management & Restoration 22:3-10
388 <https://doi.org/10.1111/emr.12522>
- 389 Dickson BG, Albano CM, Anantharaman R, Beier P, Fargione J, Graves TA, Gray ME, Hall
390 KR, Lawler JJ, Leonard PB (2019) Circuit theory applications to connectivity science and
391 conservation. Conservation Biology 33(2):239-249 <https://doi.org/10.1111/cobi.13230>
- 392 Dormann CF (2007) Promising the future? Global change projections of species distributions.
393 Basic and Applied Ecology 8(5):387-397 <https://doi.org/10.1016/j.baae.2006.11.001>
- 394 Dormann CF, Calabrese JM, Guillera Arroita G, Matechou E, Bahn V, Bartoń K, Beale CM,
395 Ciuti S, Elith J, Gerstner K (2018) Model averaging in ecology: a review of Bayesian,
396 information theoretic, and tactical approaches for predictive inference. Ecological
397 Monographs 88(4):485-504 <https://doi.org/10.1002/ecm.1309>
- 398 Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B,
399 Lafourcade B, Leitaó PJ (2013) Collinearity: a review of methods to deal with it and a

400 simulation study evaluating their performance. *Ecography* 36(1):27-46

401 <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

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

403 global land areas. *International Journal of Climatology* 37(12):4302-4315

404 <https://doi.org/10.1002/joc.5086>

405 Filz KJ, Engler JO, Stoffels J, Weitzel M, Schmitt T (2013) Missing the target? A critical

406 view on butterfly conservation efforts on calcareous grasslands in south-western Germany.

407 *Biodiversity and Conservation* 22(10):2223-2241 <https://doi.org/10.1007/s10531-012-0413-0>

408 Finch D, Corbacho DP, Schofield H, Davison S, Wright PG, Broughton RK, Mathews F

409 (2020) Modelling the functional connectivity of landscapes for greater horseshoe bats

410 *Rhinolophus ferrumequinum* at a local scale. *Landscape Ecology* 35(3):577-589

411 <https://doi.org/10.1007/s10980-019-00953-1>

412 Geyle HM, Braby MF, Andren M, Beaver EP, Bell P, Byrne C, Castles M, Douglas F, Glatz

413 RV, Haywood B (2021) Butterflies on the brink: identifying the Australian butterflies

414 (Lepidoptera) most at risk of extinction. *Austral Entomology*

415 <https://doi.org/10.1111/aen.12525>

416 Grafius DR, Corstanje R, Siriwardena GM, Plummer KE, Harris JA (2017) A bird's eye

417 view: using circuit theory to study urban landscape connectivity for birds. *Landscape*

418 *Ecology* 32(9):1771-1787 <https://doi.org/10.1007/s10980-017-0548-1>

419 Hastie T, Tibshirani R, Buja A (1994) Flexible discriminant analysis by optimal scoring.

420 *Journal of the American Statistical Association* 89(428):1255-1270

421 <https://doi.org/10.1080/01621459.1994.10476866>

- 422 Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling. 3.4-5
- 423 IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working
424 Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change
425 Masson-Delmotte V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen,
426 L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K.
427 Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou. Cambridge University Press. In
428 Press.
- 429 Jackson CR, Marnewick K, Lindsey PA, Røskoft E, Robertson MP (2016) Evaluating habitat
430 connectivity methodologies: a case study with endangered African wild dogs in South Africa.
431 Landscape Ecology 31(7):1433-1447 <https://doi.org/10.1007/s10980-016-0342-5>
- 432 Jones ME, Bain GC, Hamer RP, Proft KM, Gardiner RZ, Dixon KJ, Kittipalawattanapol K,
433 Zepeda de Alba AL, Ranyard CE, Munks SA (2021) Research supporting restoration aiming
434 to make a fragmented landscape ‘functional’ for native wildlife. Ecological Management &
435 Restoration 22:65-74 <https://doi.org/10.1111/emr.12504>
- 436 Kass JM, Anderson RP, Espinosa Lucas A, Juárez Jaimes V, Martínez Salas E, Botello F,
437 Tavera G, Flores Martínez JJ, Sánchez Cordero V (2020) Biotic predictors with
438 phenological information improve range estimates for migrating monarch butterflies in
439 Mexico. Ecography 43(3):341-352 <https://doi.org/10.1111/ecog.04886>
- 440 Kirk H, Threlfall C, Soanes K, Ramalho C, Parris K, Amati M, Bekessy S, Mata L (2018)
441 Improving connectivity for biodiversity across the City of Melbourne: A framework for
442 evaluating and planning management actions. Report prepared for the City of Melbourne
443 Urban Sustainability Branch.
- 444 Kuhn M (2021) caret: Classification and Regression Training. 6.0-86

- 445 Kutt AS, Dickson CR, Quarmby J, Kingdom D, Hamer RP (2021) Evaluating predictors of
446 Ptunarra Brown Butterfly *Oreixenica ptunarra* abundance on a conservation reserve to refine
447 future monitoring. *Ecological Management & Restoration* <https://doi.org/10.1111/emr.12544>
- 448 Laliberté J, St-Laurent M-H (2020) Validation of functional connectivity modeling: The
449 Achilles' heel of landscape connectivity mapping. *Landscape and Urban Planning*
450 202:103878 <https://doi.org/10.1016/j.landurbplan.2020.103878>
- 451 Li X, Chen G, Liu X, Liang X, Wang S, Chen Y, Pei F, Xu X (2017) A new global land-use
452 and land-cover change product at a 1-km resolution for 2010 to 2100 based on human–
453 environment interactions. *Annals of the American Association of Geographers* 107(5):1040-
454 1059 <https://doi.org/10.1080/24694452.2017.1303357>
- 455 Liang J, Ding Z, Jiang Z, Yang X, Xiao R, Singh PB, Hu Y, Guo K, Zhang Z, Hu H (2021)
456 Climate change, habitat connectivity, and conservation gaps: a case study of four ungulate
457 species endemic to the Tibetan Plateau. *Landscape Ecology* 36(4):1071-1087
458 <https://doi.org/10.1007/s10980-021-01202-0>
- 459 Littlefield CE, Krosby M, Michalak JL, Lawler JJ (2019) Connectivity for species on the
460 move: supporting climate-driven range shifts. *Frontiers in Ecology and the Environment*
461 17(5):270-278 <https://doi.org/10.1002/fee.2043>
- 462 Malakoutikhah S, Fakheran S, Hemami MR, Tarkesh M, Senn J (2020) Assessing future
463 distribution, suitability of corridors and efficiency of protected areas to conserve vulnerable
464 ungulates under climate change. *Diversity and Distributions* 26(10):1383-1396
465 <https://doi.org/10.1111/ddi.13117>

- 466 McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model
467 connectivity in ecology, evolution, and conservation. *Ecology* 89(10):2712-2724
468 <https://doi.org/10.1890/07-1861.1>
- 469 Miao BG, Peng YQ, Yang DR, Kubota Y, Economo EP, Liu C (2020) Climate and land use
470 interactively shape butterfly diversity in tropical rainforest and savanna ecosystems of
471 southwestern China. *Insect science* 28(4):1109-1120 [https://doi.org/10.1111/1744-
472 7917.12824](https://doi.org/10.1111/1744-7917.12824)
- 473 Minachilis K, Kougioumoutzis K, Petanidou T (2021) Climate change effects on multi-taxa
474 pollinator diversity and distribution along the elevation gradient of Mount Olympus, Greece.
475 *Ecological Indicators* 132:108335 <https://doi.org/10.1016/j.ecolind.2021.108335>
- 476 Miranda LdS, Awade M, Jaffé R, Costa WF, Trevelin LC, Borges RC, de Brito RM, Tambosi
477 LR, Giannini TC (2021) Combining connectivity and species distribution modeling to define
478 conservation and restoration priorities for multiple species: a case study in the Eastern
479 Amazon. *Biological Conservation* 257:109148 <https://doi.org/10.1016/j.biocon.2021.109148>
- 480 Mitchell MG, Bennett EM, Gonzalez A (2013) Linking landscape connectivity and
481 ecosystem service provision: current knowledge and research gaps. *Ecosystems* 16(5):894-
482 908 <https://doi.org/10.1007/s10021-013-9647-2>
- 483 Morán Ordóñez A, Briscoe NJ, Wintle BA (2018) Modelling species responses to extreme
484 weather provides new insights into constraints on range and likely climate change impacts for
485 Australian mammals. *Ecography* 41(2):308-320 <https://doi.org/10.1111/ecog.02850>
- 486 Mukherjee T, Sharma LK, Kumar V, Sharief A, Dutta R, Kumar M, Joshi BD, Thakur M,
487 Venkatraman C, Chandra K (2021) Adaptive spatial planning of protected area network for

488 conserving the Himalayan brown bear. *Science of the Total Environment* 754:142416
489 <https://doi.org/10.1016/j.scitotenv.2020.142416>

490 Ofori BY, Stow AJ, Baumgartner JB, Beaumont LJ (2017) Combining dispersal, landscape
491 connectivity and habitat suitability to assess climate-induced changes in the distribution of
492 Cunningham's skink, *Egernia cunninghami*. *PLOS One* 12(9):e0184193
493 <https://doi.org/10.1371/journal.pone.0184193>

494 Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on
495 terrestrial biota. *Bulletin of the American Meteorological Society* 81(3):443-450
496 [https://doi.org/10.1175/1520-0477\(2000\)081<0443:IOEWAC>2.3.CO;2](https://doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2)

497 Potts SG, Ngo HT, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J,
498 Vanbergen A (2016) The assessment report of the Intergovernmental Science-Policy Platform
499 on Biodiversity and Ecosystem Services on pollinators, pollination and food production.
500 Bonn, Germany, Secretariat of the Intergovernmental Science-Policy Platform on
501 Biodiversity and Ecosystem Services

502 Ren J, Lee SD, Chen X, Kao B, Cheng R, Cheung D Naive bayes classification of uncertain
503 data. In: 2009 Ninth IEEE International Conference on Data Mining, 2009. IEEE, p. 944-949

504 Rodrigues RG, Srivathsa A, Vasudev D (2021) Dog in the matrix: Envisioning countrywide
505 connectivity conservation for an endangered carnivore. *Journal of Applied Ecology*
506 <https://doi.org/10.1111/1365-2664.14048>

507 Roever CL, Van Aarde RJ, Leggett K (2013) Functional connectivity within conservation
508 networks: Delineating corridors for African elephants. *Biological Conservation* 157:128-135
509 <https://doi.org/10.1016/j.biocon.2012.06.025>

510 Rudnick D, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps C, Gerber LR, Hartter JN,
511 Jenness JS, Kintsch J (2012) The role of landscape connectivity in planning and
512 implementing conservation and restoration priorities. Issues in Ecology. Report No. 16,
513 Ecological Society of America. Washington, DC.

514 Samways MJ, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS,
515 Gaigher R, Habel JC, Hallmann CA (2020) Solutions for humanity on how to conserve
516 insects. Biological Conservation 242:108427 <https://doi.org/10.1016/j.biocon.2020.108427>

517 Sands DP (2018) Important issues facing insect conservation in Australia: now and into the
518 future. Austral Entomology 57(2):150-172 <https://doi.org/10.1111/aen.12342>

519 Sazli MH (2006) A brief review of feed-forward neural networks. Communications Faculty
520 of Sciences University of Ankara Series A2-A3 Physical Sciences and Engineering 50(01)
521 https://doi.org/10.1501/commua1-2_0000000026

522 Stewart FE, Darlington S, Volpe JP, McAdie M, Fisher JT (2019) Corridors best facilitate
523 functional connectivity across a protected area network. Scientific Reports 9(1):1-9
524 <https://doi.org/10.1038/s41598-019-47067-x>

525 Thackway R (2018) Land Use in Australia: Past, Present and Future. ANU Press

526 Venter O, Sanderson EW, Magrach A, Allan JR, Beher J, Jones KR, Possingham HP,
527 Laurance WF, Wood P, Fekete BM, Levy MA, Watson JE (2018) Last of the Wild Project,
528 Version 3 (LWP-3): 2009 Human Footprint, 2018 Release <https://doi.org/10.7927/H46T0JQ4>

529 Wang SW, Gebru BM, Lamchin M, Kayastha RB, Lee W-K (2020) Land use and land cover
530 change detection and prediction in the Kathmandu district of Nepal using remote sensing and
531 GIS. Sustainability 12(9):3925 <https://doi.org/10.3390/su12093925>

Wang Z, Huang Y, Pierce NE (2019) Radio telemetry helps record the dispersal patterns of birdwing butterflies in mountainous habitats: Golden Birdwing (*Troides aeacus*) as an example. *Journal of Insect Conservation* 23(4):729-738 <https://doi.org/10.1007/s10841-019-00167-5>

Warren MS, Maes D, van Swaay CA, Goffart P, Van Dyck H, Bourn NA, Wynhoff I, Hoare D, Ellis S (2021) The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences* 118(2) <https://doi.org/10.1073/pnas.2002551117>

Winfrey R, Bartomeus I, Cariveau DP (2011) Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics* 42:1-22 <https://doi.org/10.1146/annurev-ecolsys-102710-145042>

Zhang C, Zhong S, Wang X, Shen L, Liu L, Liu Y (2019a) Land use change in coastal cities during the rapid urbanization period from 1990 to 2016: a case study in Ningbo City, China. *Sustainability* 11(7):2122 <https://doi.org/10.3390/su11072122>

Zhang Y, Clauzel C, Li J, Xue Y, Zhang Y, Wu G, Giraudoux P, Li L, Li D (2019b) Identifying refugia and corridors under climate change conditions for the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Hubei Province, China. *Ecology and evolution* 9(4):1680-1690 <https://doi.org/10.1002/ece3.4815>