# Landscapes associated with Japanese encephalitis virus reflect the functional biogeography of waterbird species across Australia and the Central Indo-Pacific region

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Abstract

Japanese encephalitis virus (JEV), a zoonotic, mosquito-borne virus, has broad circulation across the Central Indo-Pacific biogeographical region (CIPBR), which recently expanded dramatically within this region across southeastern Australia over the summer of 2021-2022. Preliminary investigation of the landscape epidemiology of the outbreaks of JEV in Australian piggeries found associations with particular landscape structure as well as ardeid species richness. The ways in which waterbird species from diverse taxonomic pools with substantial functional variation might couple with JEV-associated landscape structure was not explored, and therefore, key questions regarding the landscape epidemiology and infection ecology of JEV remain unanswered. Moreover, given the established presence of JEV within the CIBPR, the extent to which waterbird species pools in JEV-associated landscapes in Australia reflect broader regional patterns in functional biogeography presents a further knowledge gap particularly with respect to potential virus dispersal via maintenance hosts. The current study investigated waterbird species presence, ecological traits, and functional diversity distribution at landscape scale, and how these aligned with confirmed JEV detections in eastern Australia and the wider CIPBR. The results showed that waterbird habitat associated with JEV detection in Australia in 2022 and more widely across the CIPBR over the last 20 years reflects a range of species representing 8 families in 4 orders (ardeids, anatids, rallids, phalacrocoracids, threskiornithids, gruids, and pelecanids). Increasing waterbird functional diversity (trait-based mean pairwise dissimilarity) was associated with landscapes delineating JEV occurrence, while only one individual trait, high hand-wing index, was consistently associated with species presence in these JEV-associated landscapes in both Australia and the broader CIPBR. This suggests that dispersal capacity among the waterbird species pools that dominate JEV-associated landscapes might be important. By taking an agnostic approach to JEV maintenance host status, this study indicates a relatively large, CIPBR-wide pool of waterbird families associated with JEV landscapes, challenging the narrow view that JEV maintenance is limited to ardeid birds. In addition, these findings highlight the potential for leveraging functional biogeography in high-risk landscapes across broad geographic extent to guide landscape-specific selection of species for JEV surveillance.

## Introduction

Japanese encephalitis virus (JEV) has circulated in the Central Indo-Pacific biogeographical region (CIPBR) for many decades(Garjito et al., 2018; Hanson et al., 2004; Johansen et al., 2000; Lopez et al., 2015). In early 2022 Japanese encephalitis virus (JEV) was detected for the first time in south-eastern regions of Australia, resulting in the declaration of a Communicable Disease Incident of National Significance. A total of 45 cases of human disease were reported, including seven fatalities(Chief Medical Officer, 2023). Outbreaks were also reported in piggeries with unprecedented wide geographic distribution, high numbers of affected piggeries, and high incidence within piggeries (Australian Department of Health and Aged Care, 2022; Mackenzie et al., 2022; Williams et al., 2022). Previous JEV occurrence in Australia had been limited to isolated cases in the Torres Strait Islands(Hanna et al., 1996) and the Cape York Peninsula of northern Queensland(Hanna et al., 1999). The extensive geographic distribution of the recent outbreaks, which included eastern and southern Australia, was of particular concern because it deviated markedly from anticipated emergence events for JEV(van den Hurk et al., 2019) and suggested broad circulation of the virus in maintenance communities prior to emergence in pigs and humans(Purnell, 2022). These outbreaks followed a long period of anomalous weather due to consecutive La Niña phases of the El Niño Southern Oscillation (ENSO), including high levels of precipitation and major flooding events across eastern Australia that generated considerable disturbance to natural communities(Bureau of Meteorology, 2021). It was hypothesised that the anomalous La Niña-associated weather patterns might have contributed to the widespread distribution of JEV outbreaks in 2022 due to modulation of vector or maintenance host population distributions(Purnell, 2022). However, a thorough investigation of landscape composition and configuration and La Niña-associated anomalies showed that landscape structure was substantially more influential to outbreak occurrence than were specific precipitation or temperature anomalies associated with La Niña(Walsh et al., 2023). Aspects of high-risk landscape structure, such as the composition of transient wetlands and the propensity to flooding, would also have been

affected by both proximal and distal precipitation events, and so La Niña-associated weather anomalies likely influenced outbreak occurrence indirectly.

Japanese encephalitis virus circulates in wild ardeid bird maintenance hosts(Bhattacharya and Basu, 2014; Buescher et al., 1959; Jamgaonkar et al., 2003; Nemeth et al., 2012; Ogata et al., 1970; Rodrigues et al., 1981; Scherer, 1959) vectored by mosquitoes (primarily *Culex annulirostris* in Australia(van den Hurk et al., 2003) and *Cx. tritaeniorhynchus* in Southeast Asia(Endy and Nisalak, 2002; Longbottom et al., 2017)) and can spillover to pigs(Baruah et al., 2018; Borah et al., 2013; Chen and Beaty, 1982; Ghimire et al., 2014; Kakkar et al., 2017; Komada et al., 1968) and humans, which are competent and non-competent hosts, respectively. Previous work has examined the distribution of ardeid species richness as a key nidus of the maintenance community, identifying a strong quadratic relationship between richness and JEV piggery outbreak occurrence, in which intermediate richness was associated with greatest risk(Walsh et al., 2023). However, only ardeid species richness was explored, and not the association between outbreaks and individual species from a broader taxonomic pool, or the influence of the structure and functional distribution of the species pool on the 2022 piggery outbreaks in Australia. The latter has not been assessed with respect to outbreaks anywhere in the CIPBR to date, despite evidence of JEV circulation across the Torres Strait Islands(Johansen et al., 2004; van den Hurk et al., 2001) and far north Queensland(van den Hurk et al., 2006), as well as in Papua New Guinea(Hanson et al., 2004; Johansen et al., 2000), for 2 decades, and in Indonesia, Malaysia, and the Philippines for several decades(Garjito et al., 2018; Lopez et al., 2015). Due to the logistics and resources required to sample birds across the vast landscapes of both Australia and the broader CIPBR, as well as the potential for extensive dispersal of maintenance hosts and vectors within the CIPBR, a better understanding of how particular species and species pools align with landscapes associated with JEV occurrence would be useful to identify target species to monitor JEV circulation in these landscapes. This could be especially useful to illuminate the full breadth of potential JEV maintenance hosts, given that a narrower perspective has typically limited

124 the scope of wild host sampling to ardeids and recent studies have provided evidence that this scope
125 should be expanded(Levesque et al., 2024; Moore et al., 2024).
126 The study of the functional ecology of viral maintenance hosts has increased in recent years
127 as a means to help identify potential hosts based on specific biological and ecological traits,
128 frequently focusing on life history due to the association between fast-living and host competence in
129 many r-selected species(Brunner et al., 2008; Cynthia J. Downs et al., 2019; Cynthia J Downs et al.,
130 2019; Han et al., 2016, 2015a, 2015b; Ostfeld et al., 2014; Plourde et al., 2017; Stephens et al., 2016).
131 These species, which are typically generalist and frequently more resilient to anthropogenic
132 pressure(Faust et al., 2018; Gibb et al., 2020; Johnson et al., 2020), tend to invest more in earlier and
133 more fecund reproductive effort, and less in immune function and adult survival(Molles, 2015). As
134 such, many of these species are also optimal hosts for pathogens(Johnson et al., 2012). Nevertheless,
135 the association between fast-living species and host competence is not universal, with some systems
136 demonstrating the opposite or ambiguous associations, such as ebolaviruses(Schmidt et al., 2019),
137 Rift Valley fever virus (RVFV)(Walsh and Mor, 2018), and Ross River virus (RRV)(Walsh, 2019). In
138 addition to life history, other host traits, including population density, diet composition, and dispersal
139 ability, can also be influential to the infection ecology of some pathogens(Gibb et al., 2020; Johnson
140 et al., 2020). Critically, relationships with species traits, particularly those relating to life history and
141 population-level transmission dynamics, have been largely neglected in bird-host pathogen systems.
142 However, a recent example demonstrated strong associations between wild avian influenza hosts
143 and life history and dispersal capacity, which is another widely distributed, albeit not vector-borne,
144 host-virus system closely associated with agricultural-wetland mosaics(Yin et al., 2023). Finally,
145 functional diversity offers a further key representation of ecological diversity, which can help to
146 inform ecological relationships beyond what is demonstrated by community composition (i.e. species
147 richness, evenness, abundance) or phylogenetic diversity alone. The extent to which landscape-scale
148 species pools diverge or converge in their biological and ecological traits can help to inform
149 environmental filtering, dispersal capacity, and biotic interactions, particularly in the context of JEV

occurrence. Notwithstanding the importance of species traits to species distributions, host functional ecology has hitherto gone unexplored with respect to JEV hosts and is, therefore, a critical knowledge gap for this system especially since the functional biogeography of waterbirds in Australia and the broader CIPBR might be directly relevant to JEV circulation across the region.

The first aim of this study was to identify how species pools mapped to JEV-associated landscapes in Australia. Specifically, we sought to determine which waterbird species (eight families of 4 avian orders) were distributed in close association with JEV piggery outbreaks, and how species pools were structured with the landscape composition and configuration of these outbreaks, to inform preliminary target host species in specific landscapes for One Health surveillance of JEV. Secondly, we aimed to determine the extent to which species pool-weighted trait means and functional diversity were coupled with JEV-associated landscapes in Australia. Finally, we aimed to determine whether species pools and their functional ecology similarly mapped to landscapes where JEV has been detected across the broader CIPBR as a whole.

164 **Material and methods**

165 Data Sources

166 *Animal data*

167 Australian piggery outbreaks (N = 54) reported to the World Organisation for Animal Health
168 (WOAH) by the Australian government between 19 January, 2022 and 4 April, 2022(World
169 Organisation For Animal Health, 2022) have been described in a previous epidemiological
170 investigation(Walsh et al., 2023). Briefly, outbreak occurrence was defined as one or more cases
171 reported at the level of the piggery. An additional 11 independently-documented JEV occurrence
172 locations (eight piggery outbreaks reported by a commercial pork producer, and 3 positive mosquito
173 pools detected through the NSW Arbovirus Surveillance and Mosquito Monitoring Program(New
174 South Wales Health, 2022)) were used to externally validate model performance. For the extended
175 CIPBR analyses, 25 additional JEV occurrence detections (9 mosquito pool detections, 14 human
176 detections, and 2 pig detections) in Papua New Guinea (n = 4)(Hanson et al., 2004; Johansen et al.,
177 2000), the Torres Strait Islands (n = 2)(Johansen et al., 2004; van den Hurk et al., 2001), the Cape York
178 Peninsula in Australia (n = 1)(van den Hurk et al., 2006), Indonesia (n = 4)(Faizah et al., 2021; Kardena
179 et al., 2024; Spicer et al., 1999), Malaysia (n = 12)(Khor et al., 2020), and the Philippines (n = 2)(Aure
180 et al., 2022) were identified from laboratory confirmed investigations that were published between
181 1997 and 2019. Geographic locations were published along with these data and latitude and
182 longitude coordinates were obtained from Google Maps when not otherwise specifically provided.
183 All reporting of these detections was available at a minimum of 2.5 arc minutes resolution.

184 The habitat suitability of extant species of waterbirds across the CIPBR was modelled using
185 5,190,722 observations of these species representing the Ardeidae, Threskiornithidae, Pelecanidae,
186 Anatidae, Rallidae, Phalacrocoracidae, Ciconiidae, Gruidae avian families that are either extant to
187 mainland Australia (n = 69 species), or the broader the CIPBR without being extant to Australia (n =
188 23 species), for a total of 92 species currently described throughout the region. Observations were
189 recorded between 1 January 2010 and 31 December 2020 and acquired from the Global Biodiversity

190 Information Facility (GBIF)(Global Biodiversity Information Facility, n.d., n.d.). The phylogenetic tree
191 of these species was obtained from the VertLife project using the Hackett backbone and constructed
192 based on the methods described by Jetz et al. (Jetz et al., 2012). Taxonomic binomial discrepancies
193 between the VertLife tree and the named species obtained from GBIF used for the species
194 distribution models described below were resolved and alternate binomials appear in parentheses in
195 Table S1, with one exception. *Porphyrio melanotus* and *Porphyrio indicus* were previously considered
196 subspecies of *Porphyrio porphyrio*, and so the former 2 species are represented by the latter
197 binomial, *Porphyrio porphyrio*, in the phylogenetic tree. Thus, all phylogenetic analyses comprise 91
198 species rather than the current full 92 species. Data obtained from the national pig herd dataset,
199 which is used in the Australian Animal Disease Spread Model, were used to quantify Australian
200 domestic pig density for the JEV models described below. This dataset comprises >8000 registered
201 pig herds of all types (including commercial, boar studs, smallholder and pig keepers)(Bradhurst et
202 al., 2015). For the rest of the CIPBR, pig density was obtained from the Gridded Livestock of the
203 World database(Robinson et al., 2014).
204 Reporting bias may affect JEV occurrence detection, whereby large commercial herds may be
205 more likely to capture and record cases due to more systematic collection of production data and
206 increased probability of disease detection in larger herds. Moreover, all JEV detections in this study
207 were associated with piggeries either directly or indirectly, from the piggery outbreak data in
208 Australia, to human outbreaks proximate to piggeries and pig sentinel and mosquito vector
209 surveillance in other parts of the CIPBR. Therefore, background points for JEV models were selected
210 proportional to pig density throughout the CIPBR to correct for potential JEV detection reporting
211 bias.
212
213 *Environmental data for habitat suitability models*
214 Land cover classification based on the European Space Agency and Climate Change Initiative
215 was used to classify wetlands(European Space Agency and Climate Change Initiative, 2017a;

Lamarche et al., 2017) and land cover(European Space Agency and Climate Change Initiative, 2017b) at 3 arc seconds in 2010, as this time point corresponded to the beginning of the period of recorded ardeid observations described above. Waterways were represented by a separate high-resolution (3 arc seconds) image produced in collaboration between CIESIN and the WorldPop project (University of Southampton et al., n.d.; WorldPop, n.d.). Mean annual precipitation, mean annual temperature, and isothermality were obtained from WorldClim (Fick and Hijmans, 2017). The Priestley-Taylor α coefficient (P-Tα) is the ratio of actual evapotranspiration to potential evapotranspiration and was used to describe water stress in the landscape(Khaldi et al., 2014; Priestley and Taylor, 1972). The P-Tα data were acquired from the Consultative Group for International Agricultural Research (CGIAR) Consortium for Spatial Information at a resolution of 30 arc seconds(Trabucco and Zomer, 2010).

*Environmental data for landscape-level metrics (Australia-only)*

All JEV outbreaks in Australia were reported to a scale of at least 5 arc minutes (~ 10 km), which thus represents the landscape-level scale of the current investigation. Land cover classes were represented using the previously validated Copernicus land cover data at 100 m resolution(Jung et al., 2020a, 2020b). The Joint Research Centre's Global Surface Water product (based on Landsat 5, 7, and 8 imagery) was used to represent high resolution (30 m) surface water seasonality in the year prior to piggery outbreaks(Joint Research Centre, n.d.; Pekel et al., 2016). Each pixel in the raster tiles represents the total number of months (0 – 12) with surface water present during 2021. The heterogeneity of water transience across the landscape was based on five derived rasters: 1) permanent surface water presence over the 12 months of 2021, 2) surface water absence over the 12 months of 2021, 3) surface water presence for 1 to 3 months of the year, 4) surface water presence for 4 to 6 months of the year, and 5) surface water presence for 7 to 9 months of the year. Water movement through and accumulation in the landscape was quantified using hydrological flow accumulation, which describes the total upland area draining into each 500m by 500m parcel and

241 was acquired from the Hydrological Data and Maps based on SHuttle Elevation Derivatives at
242 multiple Scales (HydroSHEDS) information system(Lehner et al., 2006).
243
244 *Waterbird trait data*
245 Bird species' diet composition and body mass were obtained from the Elton Traits
246 database(Wilman et al., 2014). Diet composition may be an important characteristic of host species
247 because this can delineate generalist versus specialist species and potential resilience to human
248 pressure(Swihart et al., 2003). Only the dietary proportions of fish and invertebrates demonstrated
249 heterogeneity among the ardeid species, so only these dietary elements were investigated. Body
250 mass is an important life history characteristic as well as being a potential modulator of immune
251 function(Cynthia J Downs et al., 2019; Cynthia J. Downs et al., 2019). Body mass was log transformed
252 prior to analysis. The TetraDENSITY database was used to obtain species mean population
253 density(Santini et al., 2018), the AVONET database was used to obtain the hand-wing index(Tobias et
254 al., 2022), and the Lislevand bird traits database was used to obtain the reproductive characteristic,
255 egg mass(Lislevand et al., 2007). These species traits were included since population density may
256 influence the dynamics of JEV circulation in populations and communities(Adler et al., 2008; Begon
257 et al., 2002; Rodríguez-Pastor et al., 2019; Thrall et al., 1995), hand-wing index has been shown to be
258 the best metric to represent bird dispersal(Kennedy et al., 2016; Lockwood et al., 1998) particularly
259 with respect to dispersal in response to climate and habitat loss(Sheard et al., 2020; Weeks et al.,
260 2023) and has been associated with other avian viral outbreaks previously(Yin et al., 2023), and egg
261 mass is an important indicator of reproductive life history. The data for population density, hand-
262 wing index, and egg mass were missing for 78%, 23%, and 29% of species, respectively, so a random
263 forest machine learning algorithm, which was previously shown to be a robust approach with low
264 error to this application(Fountain-Jones et al., 2019; Penone et al., 2014), was used to impute the
265 missing data. The missForest package was used to implement the algorithm(Stekhoven, 2022).
266

## Statistical Analysis

*Species distribution modelling*

The habitat suitability of 92 waterbird species present in the CIPBR (69 extant in mainland Australia, 23 extant in the CIPBR but not in Australia) was modelled using the GBIF data described above (Table S1). Habitat suitability models were based on ensembles of boosted regression trees (BRT), random forests (RF), and generalised additive models (GAM), each with spatial block cross-validation at fine-scale (30 arc seconds). The calibration areas for the models were based on a buffer of 500 km for the species presence points. Geographically structured spatial partitions were used to select background points. Observation data were thinned so that only one observation per pixel was included in the analysis to avoid overfitting (Table S1). Environmental features in each suitability model comprised mean annual temperature, mean annual precipitation, isothermality, P-T$\alpha$, and proximity to surface water, forest, shrubland, grassland, aquatic vegetation, and cropland. Each model was evaluated according to the model's omission rate, true skill statistic, and the area under the receiver operating characteristic curve (AUC). Suitability estimates for each species were then derived from an ensemble of the three models (BRT, RF, and GAM) using their average maximum sensitivity and specificity.

Subsequently, the species pool available for community assembly was estimated with each species as follows. Each 1 $km^2$ pixel of each species' habitat suitability estimate that was greater than or equal to the true skill statistic (TSS)(Allouche et al., 2006) was classified as present and summed across all pixels within the 5 arc minute landscape parcel. The TSS was used to designate each parcel as present or absent based on the habitat suitability because it has been shown to be independent of prevalence(Allouche et al., 2006). This summed metric thus provided an estimate for landscape-level species presence available to community assembly for each species from within the species pool at each particular landscape parcel. For each species, this "species pool presence" (SPP) could range from 0, indicating the species was not expected to be present in any 1 $km^2$ pixels within the 5 arc minute landscape parcel, to 100 indicating the species was expected to be present in all 1 $km^2$ pixels

293 within the landscape parcel. The SPP was thus calculated for each of the 92 waterbird species
294 interrogated and represents the metric used to denote species presence at landscape scale, and was
295 used for "abundance" weighting of the mean pairwise dissimilarity described below although this is
296 not intended to represent species abundance. Direct measurement of community composition,
297 including species abundance and relative abundance, was not possible in the current study since
298 community structure was not observed directly at the appropriate local scale. Instead, the SPP
299 provides the degree of available habitat for each species from within the pool at each landscape
300 parcel. The flexsdm package provided a complete streamlined framework to construct the calibration
301 areas and spatial block partitions, select background points, fit all species distribution models, and
302 derive and evaluate the habitat suitability ensembles as described above(Velazco et al., 2022).
303
304 *Landscape metric analysis (Australia-only)*
305 The metrics used to delineate high-risk landscape structure in the Australian context have
306 been described in detail previously in an analysis of the landscape composition and configuration
307 associated with Australian JEV outbreaks in piggeries(Walsh et al., 2023). Briefly, increasing cultivated
308 land and fragmented grassland were both associated with JEV outbreaks and these were computed
309 as follows. Total cultivated land composition was computed by summing the area of all crop patches
310 in each landscape parcel (landscape-level scale of 5 arc minutes). Grassland fragmentation was
311 assessed by measuring mean patch edge relative to patch area for all grassland patches in each
312 parcel using the related circumscribing circle (RCC). The RCC metric has been shown to be robust to
313 patch size(Csorba and Szabo, 2012) in contrast to the perimeter-to-area ratio (PAR), wherein similarly
314 shaped patches can give different values for different sizes and can translate to significant error when
315 summarising PAR at landscape scale(Csorba and Szabo, 2012). These composition and configuration
316 metrics were previously computed for all land cover classes as referenced above, but only those
317 shown to be associated with JEV outbreak occurrence are investigated with respect to ardeid species

here as this was the stated aim of the current study. The landscapemetrics package(Hesselbarth et al., 2019) was used to calculate RCC in R v. 4.3.1.

*Functional metrics for species traits*

As a crude measure of the species pool-weighted trait means at landscape scale, the commonly used community-weighted mean, was calculated for each trait among all species identified as present (as described above under habitat suitability modelling) within each landscape parcel(Laliberte and Legendre, 2010; Lavorel et al., 2008). These "pool-weighted means (PWMs)" are not intended to represent local community trait means, but rather to identify whether any species traits shared among the pool at landscape scale stood out as potentially influential for community assembly (though assembly itself is not described), and particularly in high-risk JEV landscapes. Mean pairwise dissimilarity (MPD) was also computed as a robust metric of functional diversity to evaluate the species pool trait heterogeneity, again quantified at landscape scale and extending across the CIPBR. The MPD was "abundance"-weighted, though, as described above, this weighting was not based on actual estimates of community-level species abundances but rather based on the number of 1 km pixels in which each species was designated present within the 10 km landscape parcel. The FD package(Laliberté et al., 2014) was used to compute weighted means for species traits, the picante package(Kembel et al., 2010) was used to compute MPD, and phytools was used to compute the phylogenetic signal (both Blomberg's K and Pagel's λ) of species traits and map continuous traits onto the phylogenetic tree(Revell, 2012) in R v. 4.3.1.

*Point process modelling*

Each of the 92 individual waterbird species' landscape-level presence within the pool was interrogated with respect to JEV detection by fitting inhomogeneous Poisson point process models (PPMs)(Baddeley et al., 2015; Baddeley and Turner, 2000). To control for potential reporting bias in outbreak surveillance, the background points used in these models were sampled proportional to

344 mean pig density, as described above. For the individual waterbird species PPMs, a simple univariate
345 PPM of JEV outbreaks was created for each of the 92 species. Similarly, for the species trait PPMs, a
346 simple univariate PPM of JEV detections was created for each species trait's PWM; however, this
347 univariate trait analysis was followed by a multiple PPM to determine which traits among the species
348 pool were independently associated with JEV outbreaks. For the CIPBR models, correlation between
349 the spatial distribution of traits was low (Pearson's $r \leq 0.66$) and all variance inflation factors were ≤
350 4.65, indicating collinearity was not a concern for the trait multiple PPM. However, for the Australia-
351 specific model the variance inflation factors indicated multicollinearity with hand-wing index and
352 underwater foraging strategy, so these two variables were fit under separate model structures. All
353 PPMs were fit at a scale of 5 arc minutes, which was the optimum scale of JEV reporting for all
354 detections included in Australia and across the CIPBR(Walsh et al., 2023). The Akaike information
355 criterion (AIC) was used to evaluate model fit. The spatstat R package was used to fit the
356 PPMs(Baddeley and Turner, 2005).
357
358 *Hierarchical modelling of species pools (Australia only)*
359 A hierarchical modelling of species communities (HMSC) framework(Ovaskainen and Abrego,
360 2020; Tikhonov et al., 2020) was used to assess species pools in relation to the specific features of
361 landscape composition and configuration that have been shown to delineate JEV outbreak risk in the
362 Australian context (Figure S1)(Walsh et al., 2023). In addition, the HMSC framework accounted for
363 the potential modulation of species presence in high-risk landscape structure by their phylogeny and
364 functional traits, associations with the latter representing species "responses" to the landscape
365 features. However these associations do not represent estimates of actual responses within
366 communities and so this interpretation must be tempered (see below). Models were fit under two
367 landscape domains: the first comprised each of the individual landscape features shown to be
368 associated with JEV outbreaks in Australian piggeries (Figure S1) and the second comprised
369 Australian JEV outbreak occurrence itself as the single landscape feature of interest. The two

separate domains were evaluated since the landscape features associated with JEV outbreaks did not explain all of the variability in JEV outbreak occurrence, indicating that there are additional unmeasured landscape features that cannot be captured by the first domain, but which may still be relevant to species presence in the landscape. The models were fit with the probit link function to represent species presence, rather than species abundance, as the former is more appropriate given the focus of investigation at landscape scale as already described above. The probit function is preferred over the logit function in HMSC models because it provides a more pragmatic fit to the hierarchical multivariate data(Ovaskainen and Abrego, 2020). These models are fitted using Markov chain Monte Carlo methods and were run here with four chains and 1000 samples each and a burn-in set to 20% of the initial samples. The adjusted $r^2$ was used to assess model fit for each of the two model domains. Model convergence was demonstrated for each species (Gelman diagnostic ≈ 1 for each species). Although interspecific interaction within communities was not observed in this study, the HMSC framework does allow for further accounting of important phylogenetic and functional influence on the sharing of space between sympatric species given environmental filtering, which cannot be evaluated with the PPMs described above. Nevertheless, it must be noted that since biotic filtering has not been directly observed, which necessarily occurs at the level of the local community, true community-level functional responses to environmental conditions are not captured at this landscape scale. Instead, these multivariate analyses allow correlative associations to be identified that are anticipated to be useful in characterising how community assembly could potentially operate in landscapes associated with JEV outbreaks, and thereby help to inform sampling targets within such landscapes so that community monitoring of JEV hosts can be systematically structured for One Health surveillance across the large geographic extent of eastern Australia. The Hmsc package(Tikhonov et al., 2020) was used for the HMSC models.

394 **Results**

395 The PPMs identified landscape-level distributions of 42 species that were associated with
396 Australian JEV outbreaks (7 ardeids, 16 anatids, 8 rallids, 5 phalacrocoracids, 5 threskiornithids, 1
397 gruid, and 1 pelecanid)(Table S2). When considering the CIPBR as a whole with additional JEV
398 detections in the Philippines, Malaysia, Indonesia, Papua New Guinea, and the Cape York Peninsula,
399 49 species of the total 92 waterbirds species evaluated were associated with JEV-associated
400 landscapes, again representing each of the eight avian families (Table S3). Of all the individual species
401 traits interrogated under the PPMs, only the PWM distributions of hand-wing index (RR = 1.273; 95%
402 C.I. 1.134 – 1.428) and underwater foraging (RR = 1.05; 95% C.I. 1.014 – 1.088) demonstrated
403 independent associations with the distribution of JEV outbreaks in the Australian context (Table S4,
404 Table 1 and Figure 1), whereas hand-wing index alone (RR = 1.17 ; 95% C.I. 1.100 – 1.246) was
405 independently associated with increasing JEV detections across the CIPBR as a whole (Table S4, Table
406 1 and Figure 2). In addition, mean pairwise dissimilarity was positively associated with JEV detections
407 in both Australia and the broader CIPBR, indicating that more functionally diverse species pools were
408 associated with JEV detections. Target maps of high suitability for Australian waterbird sampling for
409 JEV One Health surveillance based on the two PPMs (one incorporating MPD and one incorporating
410 foraging strategy) is presented in Figure 3.

411 The Australian-specific HMSC model was in close agreement with respect to the structure of
412 the species pool, identifying similar species presences associated with JEV occurrence as those
413 identified by the PPMs(Figure 4). The median adjusted $r^2$ for the landscape feature-based model and
414 JEV-based model was 15.8% and 25.0%, respectively. The HMSC model showed that whilst some
415 high-risk landscape features were common to almost all waterbird species (the presence of transient
416 wetlands and proximity to waterways, as expected), other high-risk features reflected much more
417 heterogenous species pools (Figure 4). By and large, species presence within these high-risk
418 landscape features did not appear closely associated with their functional traits after having
419 accounted for phylogenetic structure, with one exception. There was a distinct association between

420 species presence in landscapes of high water flow accumulation and higher hand-wing index (left
421 panel, Figure 5). Furthermore, interrogating landscapes defined solely by their JEV outbreak
422 occurrence, rather than the individual landscape features associated with outbreaks, showed that
423 species presence in landscapes characterised by outbreak occurrence was also associated with
424 greater species hand-wing index (right panel, Figure 5).

425 Interestingly, further insight about the broad associations between hand-wing index and
426 species presence in JEV-associated landscapes in Australia and across the CIPBR was provided when
427 this trait was mapped to the waterbird phylogeny (Figure 6), and both Blomberg's K ($K = 0.345$; $p =$
428 $0.001$) and Pagel's $\lambda$ ($\lambda = 0.874$; $p < 0.00001$) showed that hand-wing index was phylogenetically
429 correlated across waterbird species. Although the ardeid family showed a moderate to high hand-
430 wing index, the anatid, threskiornothid, and phalacrocoracid families showed substantively higher
431 hand-wing index, as did a couple of individual stork species (Ciconiidae) and pelicans (Pelecanidae).
432

433 **Discussion**

434 This study describes waterbird presence and the functional structure of species pools at
435 landscape scale to inform JEV surveillance in high-risk landscapes for JEV circulation in Australia, as
436 well as providing evidence that these associations might reflect the functional biogeography (hand-
437 wing index) of species presence relative to JEV circulation.

438 Although several ardeid species were strongly associated with the distribution of JEV
439 detections in Australia and across the CIPBR, species presence was neither limited to nor dominated
440 by ardeids, challenging conventional wisdom and suggesting that JEV surveillance should include a
441 broader range of potential waterbird hosts. Hand-wing index was associated with species presence in
442 landscapes demarcated by JEV occurrence in both Australia and the broader CIPBR, and
443 simultaneously demonstrated an association with species presence in areas with transient wetlands
444 in Australia, which may indicate functional modulation of species with respect to this high-risk JEV-
445 associated landscape feature. Contrary to expectation, increasing functional divergence among the
446 species pools was associated with JEV detections. For the purposes of wildlife surveillance
447 development in Australia, these findings suggest that whilst high-risk JEV landscapes can vary with
448 respect to the waterbird species present, JEV surveillance across broad regions of eastern and
449 southern Australia can be informed using a combination of landscape structure and targeting of
450 individual species in these landscapes (see Table S2 for full list of associated species). Moreover, a
451 more nuanced consideration of the functional biogeography of waterbird species across Australia
452 and the CIPBR suggests that broader, regional surveillance development may benefit from
453 considering target species with trait profiles that favour dispersal.

454 The extraordinarily broad geographic distribution of JEV outbreaks in Australia makes
455 developing a representative, systematic sampling strategy to answer key maintenance host ecology
456 questions exceedingly challenging. This study informs the development of such a sampling strategy,
457 describing waterbird presence as a function of the available species pool and enabling species
458 presence to be directly evaluated with respect to the landscape structure associated with JEV

459 outbreaks, and therefore that landscape structure can inform species selection for surveillance.
460 Moreover, by further considering species presence across the regional as whole, this study was able
461 to interrogate functional traits relevant to pathogen transmission within the context of known
462 regional transmission of JEV. The current study identified several species that were individually
463 associated with JEV in Australia and across the CIPBR and found that many of these species represent
464 families other than the Ardeidae, suggesting that conventional understanding JEV maintenance hosts
465 may be too narrow in scope. Moreover, in the Australian context, species presence is likely to be
466 heterogeneous across the different landscape features associated with JEV outbreaks, and these
467 associations can reflect differences in functional traits (e.g. dispersal capacity) that are relevant to
468 both arbovirus transmission and response to environmental variation at landscape scale (i.e.
469 flooding).

470 Associations between the dominant traits of species present in the landscape species pool
471 may provide insight into potential drivers of species structure in landscapes delineating JEV risk. For
472 example, landscapes associated with JEV occurrence were also characterised by species
473 demonstrating a high level of dispersal capacity, as indicated by greater hand-wing index. This may
474 indicate the importance of dispersal among species in the context of seasonal or transient wetlands,
475 which were strongly associated with species presence in the current study, and Australian JEV
476 outbreaks previously(Walsh et al., 2023). Such a scenario is supported by analyses of population
477 structure among birds in Australia following La Niña precipitation anomalies(Englert Duursma et al.,
478 2018; Purnell, 2022), and reflects more general evidence for the importance of hand-wing index as
479 an indicator of dispersal capacity in response to climate gradients and habitat
480 fragmentation(Kennedy et al., 2016; Sheard et al., 2020; Weeks et al., 2023). Moreover, dispersal
481 capacity as indicated by hand-wing index has also been shown to be associated with bird host status
482 and landscape-level outbreak occurrence, albeit for a different viral pathogen but one that,
483 nevertheless, involves waterbirds in agricultural-wetland mosaics (Yin et al., 2023). Furthermore, the
484 strong association between hand-wing index and JEV landscapes in the current study extended to

485 the whole of the CIPBR, although this investigation was not able to deconstruct the composition and
486 configuration of these landscapes for the region as a whole as it did for Australia, specifically.
487 Interestingly, the two broad-scale multiple PPM approaches (Australia and CIPBR) generally agreed
488 with respect to the best fitting models comprising hand-wing index and MPD, and both also
489 univariately identified associations with population density and foraging strategy. The association
490 between JEV detection and higher population density is not surprising as this may reflect pathogen
491 transmission dynamics(Adler et al., 2008; Begon et al., 2002; Thrall et al., 1995), but it did not persist
492 after having accounted for hand-wing index, MPD and foraging strategy in the Australian context and
493 hand-wing index and MPD in the CIPBR context. It should also be noted that the association between
494 hand-wing index and species presence in high-risk landscapes was not an artifact of body mass
495 because these traits were not correlated (Pearson's r = -0.21), which is as expected since hand-wing
496 index accounts for body size(Lockwood et al., 1998). While these findings are intriguing, it is critical
497 to emphasise that they are only correlative of possible drivers of community assembly at landscape
498 scale and do not describe realised community structure or specific modulation of environmental (or
499 biotic) filtering by species traits. It is not possible to infer local community composition or functional
500 responses to environmental conditions from the data presented here. Rather, the true utility of this
501 work is to describe preliminary, evidence-based, configurations of waterbird species pools for the
502 coupling of high-risk JEV landscape structure with potential maintenance hosts across extraordinarily
503 broad geographic extent, and thereby inform the development of broad-scale sampling strategies for
504 One Health JEV surveillance, specifically for Australia but with potential impact for the broader
505 region.

506 Beyond the implications of these findings for potential wild bird surveillance programs, there
507 may be potential utility for the design of arbovirus surveillance programs by local health authorities
508 in Australia. Monitoring sites is often informed by historic arbovirus activity or according to potential
509 mosquito and waterbird habitats. Consideration of wildlife hosts, and concomitant traits, in specific
510 landscapes may provide additional information in identifying appropriate arbovirus surveillance

511 locations. Nevertheless, a thorough investigation of mosquito communities and vector-host
512 interactions between mosquito and waterbird communities, particularly across heterogenous
513 features of high-risk landscapes, will also be essential for maximally beneficial surveillance output.
514 The current study was not able to interrogate vector communities specifically, and as such this
515 remains a key knowledge gap in the infection ecology of JEV.

516 In addition to the specific constraints to interpretation of the results described above,
517 further description of additional limitations is included below. Firstly, both the recording of bird
518 observations and the reporting of piggery outbreaks in Australia and other JEV detections across the
519 CIPRB may be affected by reporting biases. We have corrected for potential biases, respectively, by
520 using spatial block partitioning in the construct of the SDMs, and sampling background points for JEV
521 occurrence proportional to mean pig density, as described above. Nevertheless, it is possible that
522 residual bias may persist. Moreover, it is important to note that the sample of JEV detections across
523 the CIPBR is small and, despite this sample being both reflective of piggeries and corrected for
524 potential reporting bias, likely reflects quite different surveillance systems to those that generated
525 the reporting for piggery outbreaks in Australia. Therefore, we emphasise that this sample is in no
526 way intended to be representative of JEV presence across the region. Rather, it is intended as a
527 rudimentary comparison to the mapping of waterbird species in Australia to evaluate whether there
528 may be a potential shared biogeography of waterbird hosts across the broader region. The primary
529 practical application of the findings for wildlife monitoring in JEV surveillance are nevertheless
530 limited to Australia. Secondly, notwithstanding the inclusion of each of the waterbird species found
531 in the CIPBR in the habitat suitability modelling, it is important to note that suitability can be
532 interpreted with respect to the fundamental niche only, because it does not include direct
533 observational evaluation of biotic interactions to more formally define the realised niche or
534 subsequent community structure. We must acknowledge that neither local biotic interactions nor
535 dispersal history are represented in this framework and should be considered in future work. Thirdly,
536 the climate measures used in the waterbird habitat suitability models were derived from decadal

537 averages from 1970 to 2000, which assumes homogeneity over this period as well as over the period
538 of bird observations from 2010 to 2020. Although the current study used these features to model the
539 influence of climate features on habitat suitability rather than specific weather events, which is
540 appropriate, we do note that, due to the rapid increase in global temperatures over the last 20 years,
541 climatic means could have already shifted by 2020 from the baseline represented by the period
542 1970-2000. Finally, previous work showed that the piggery outbreaks were not associated with feral
543 pigs(Walsh et al., 2023). Nevertheless, JEV has been identified in feral pigs in Australia, albeit only
544 very sporadically(Australian Veterinary Association, 2023). As such, it is possible that there may be
545 multiple landscapes of JEV risk, both within Australia and the broader CIPBR: those pertaining to
546 domestic piggeries and those pertaining to feral pig habitat. If the latter are in fact present and
547 represent impactful nidi of JEV circulation, then different surveillance programs targeting different
548 maintenance host communities may be required.

549 **Conclusions**

550 This study has identified a breadth of waterbird species in association with particular
551 configurations of landscape risk that extends well beyond the Ardeidae family, the taxon to which
552 epidemiological and ecological investigations of JEV maintenance hosts are typically constrained.
553 Moreover, the findings relate species presence in JEV-associated landscapes to waterbird functional
554 biogeography across the CIPBR, highlighting dispersal capacity in particular. Although preliminary, it
555 is anticipated that together these results can help to inform an evidence-based approach to JEV
556 surveillance development that can provide a more efficient and productive yield than a simple
557 random or convenience-based approach to maintenance host sampling, particularly given the wide
558 geographic extent in which JEV outbreaks occurred across the region. As wild bird monitoring
559 progresses and local community structure becomes better articulated with respect to JEV circulation,
560 we expect that the scope of JEV maintenance understanding will be updated to reflect currently
561 unrecognised local heterogeneities in landscape and community composition, as well as novel
562 maintenance hosts.

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Table 1. Regression coefficients and 95% confidence intervals for the associations between Japanese encephalitis virus outbreaks and species traits as derived from multiple inhomogeneous Poisson models for Australia alone (A) and the Central Indo-Pacific biogeographical region (CIPBR) as a whole (B).

| **Landscape species pool weighted traits** | **AIC** | **Estimate** | **95% confidence interval** |
|---|---|---|---|
| **A. Australia-specific** | | | |
| *Null model* | 236.75 | | |
| *Model 1* | 212.06 | | |
| Hand-wing index | | 1.297 | 1.158 – 1.453 |
| Mean pairwise dissimilarity | | 9.312 | 2.205 – 16.419 |
| *Model 2* | 213.91 | | |
| Hand-wing index | | 1.273 | 1.134 – 1.428 |
| Forage strategy – underwater | | 1.050 | 1.014 – 1.088 |
| **B. CIPBR** | | | |
| *Null model* | 838.56 | | |
| Hand-wing index | 479.47 | 1.17 | 1.100 – 1.246 |
| Mean pairwise dissimilarity | | 2.302 | 1.127 – 4.704 |

990 Figure legends

991 Figure 1. The distribution of the pool-weighted means (PWMs) of species traits for those traits that
992 were associated with Japanese encephalitis outbreaks in the univariate point process models
993 (proportion underwater foraging strategy, hand-wing index, and population density) and mean
994 pairwise dissimilarity (MPD) across Australia. The overlaid points represent the locations of the JEV
995 piggery outbreaks.

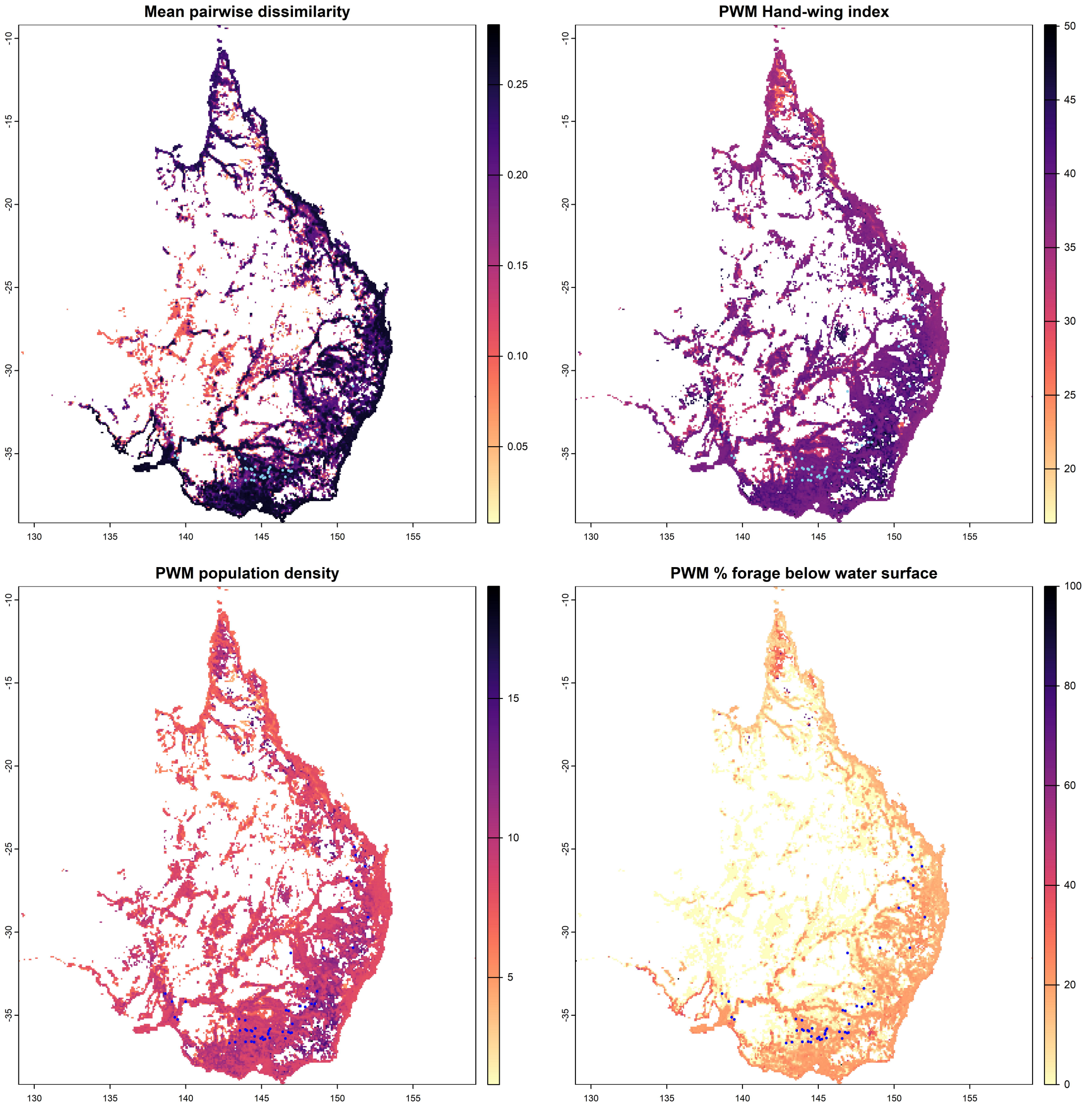
996 Figure 2. The distribution of the pool-weighted means (PWMs) of species traits for those traits that
997 were associated with Japanese encephalitis outbreaks in the univariate point process models (egg
998 mass, proportion of the diet comprising plants, proportion underwater foraging strategy, hand-wing
999 index, and population density) and mean pairwise dissimilarity (MPD) across the Central Indo-Pacific
1000 biogeographical region. The overlaid points represent the locations of the JEV piggery outbreaks.

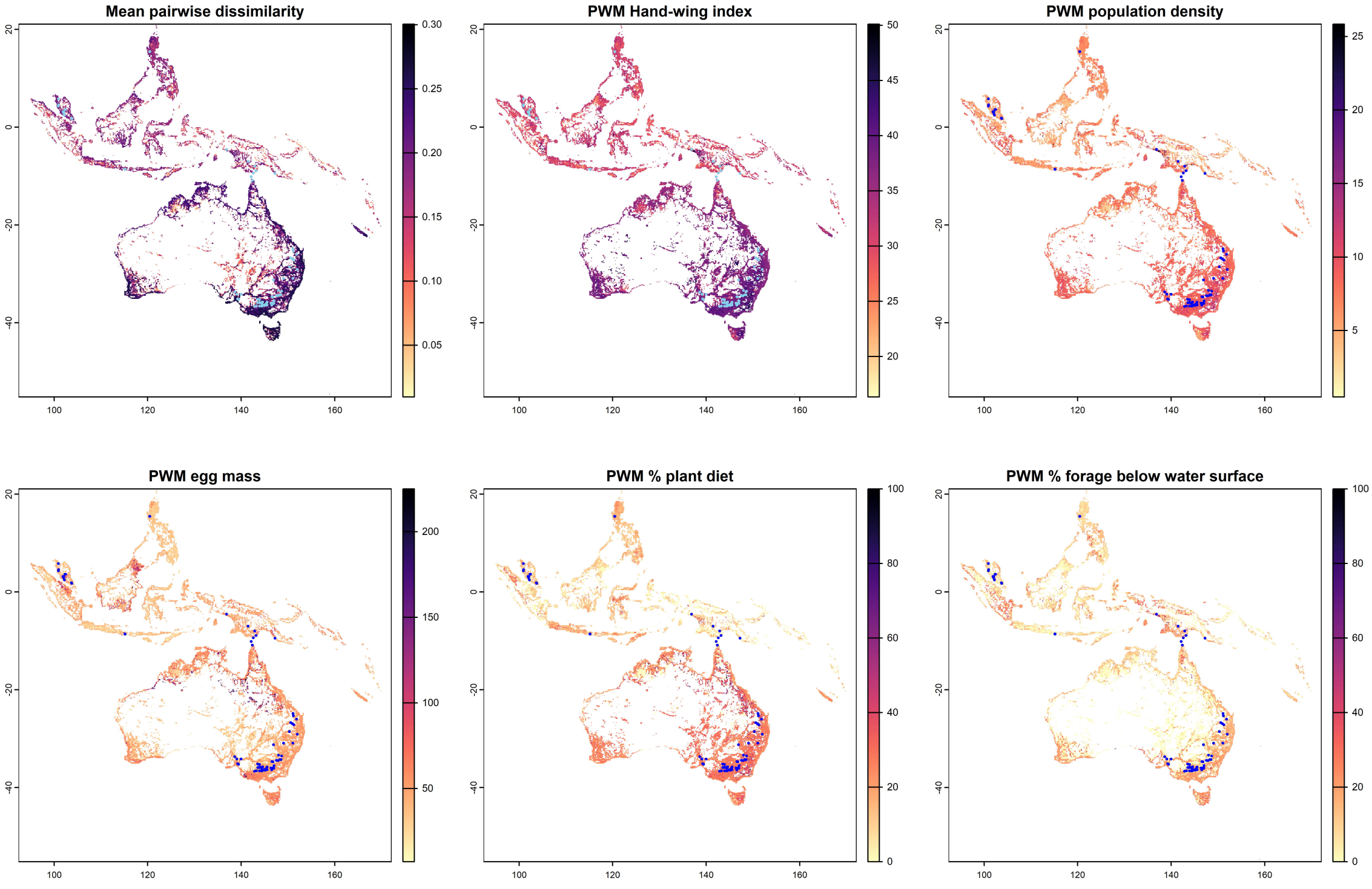
1001 Figure 3. Suggested landscape sampling for Australia based on JEV outbreak intensity estimates as a
1002 function of waterbird species traits. The distribution of JEV predicted intensity is presented in the
1003 centre panels by decile, whereas the left and right panels represent the lower and upper 95%
1004 confidence limits for the predicted intensities, respectively. Predictions are based on the best fitting
1005 and performing inhomogeneous Poisson point process model (Table 1A).

1006 Figure 4. The associations between each species and the landscape features under two model
1007 structures using hierarchical modelling of species communities (HMSC). The first HMSC model (top
1008 panel) shows associations as positive, negative, or neutral "responses" of each species on the y-axis
1009 to each landscape feature associated with JEV outbreaks on the x-axis. The second HMSC model
1010 (bottom panel) shows these associations for JEV outbreak occurrence only and no other landscape
1011 features.

1012 Figure 5. The association between species traits and the landscape features, representing
1013 modulation of species "responses" to the landscape features, under two model structures using
1014 hierarchical modelling of species communities (HMSC). The first HMSC model (left panel) shows
1015 associations as positive, negative, or neutral "modulators" for each trait on the y-axis of each
1016 landscape feature associated with JEV outbreaks on the x-axis. The second HMSC model (right panel)
1017 shows these associations for JEV outbreak occurrence only and no other landscape features.

1018 Figure 6. Mapping of hand-wing index onto the phylogenetic tree for 91 waterbird species evaluated
1019 across the Central Indo-Pacific biogeographical region.


Mean pairwise dissimilarity
0.25
0.20
0.15
0.10
0.05
PWM Hand-wing index
50
45
40
35
30
25
20
PWM population density
15
10
5
PWM % forage below water surface
100
80
60
40
20
0
-10
-15
-20
-25
-30
-35
130
135
140
145
150
155


Mean pairwise dissimilarity
PWM Hand-wing index
PWM population density
PWM egg mass
PWM % plant diet
PWM % forage below water surface
20
0
-20
-40
100
120
140
160
0.30
0.25
0.20
0.15
0.10
0.05
50
45
40
35
30
25
20
25
20
15
10
5
200
150
100
50
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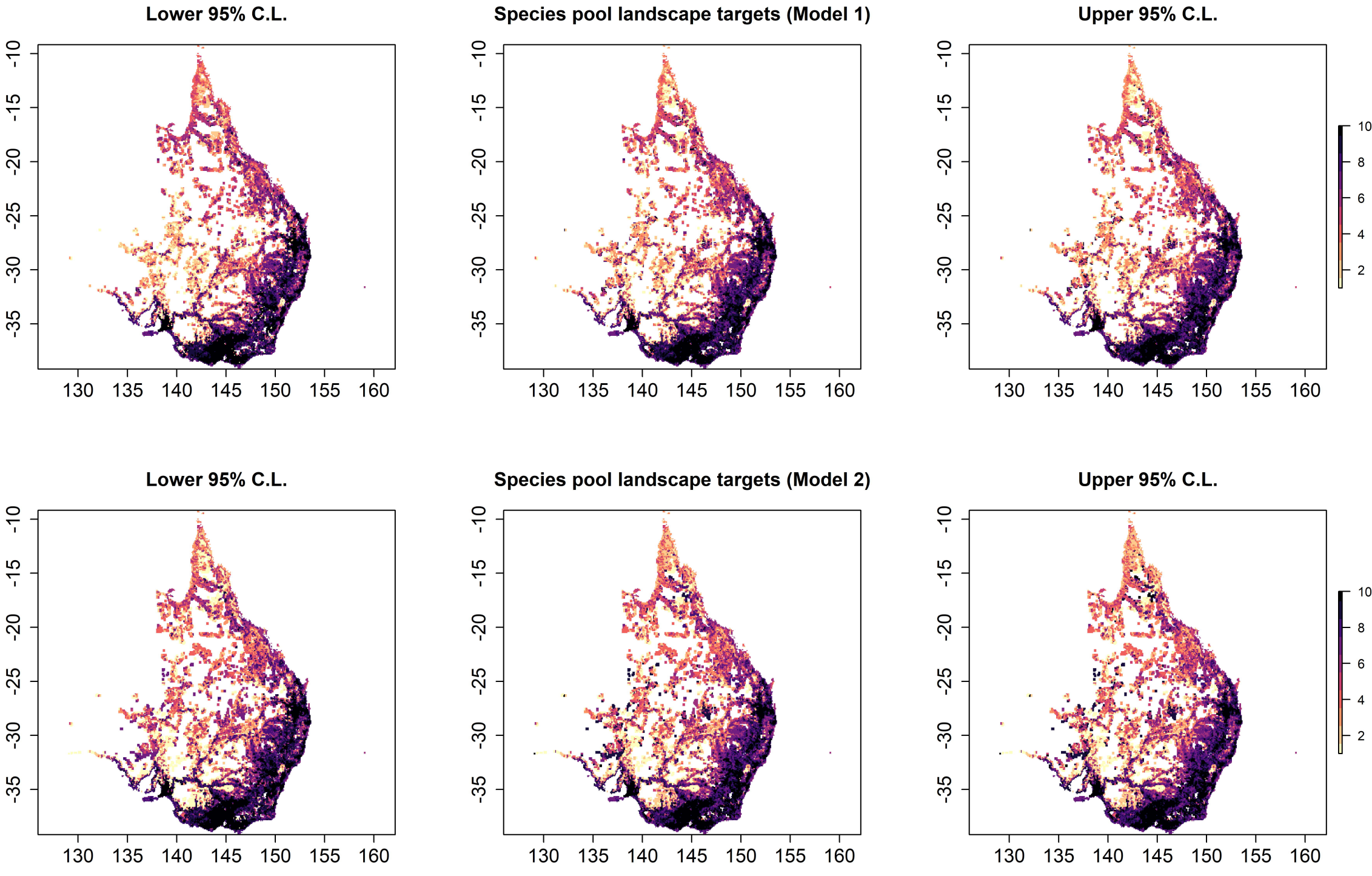
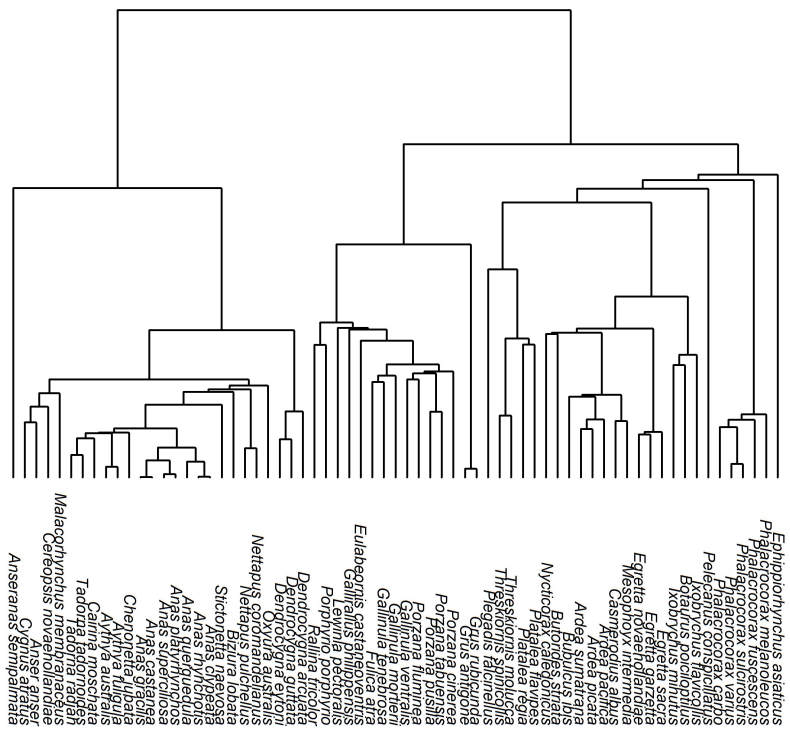
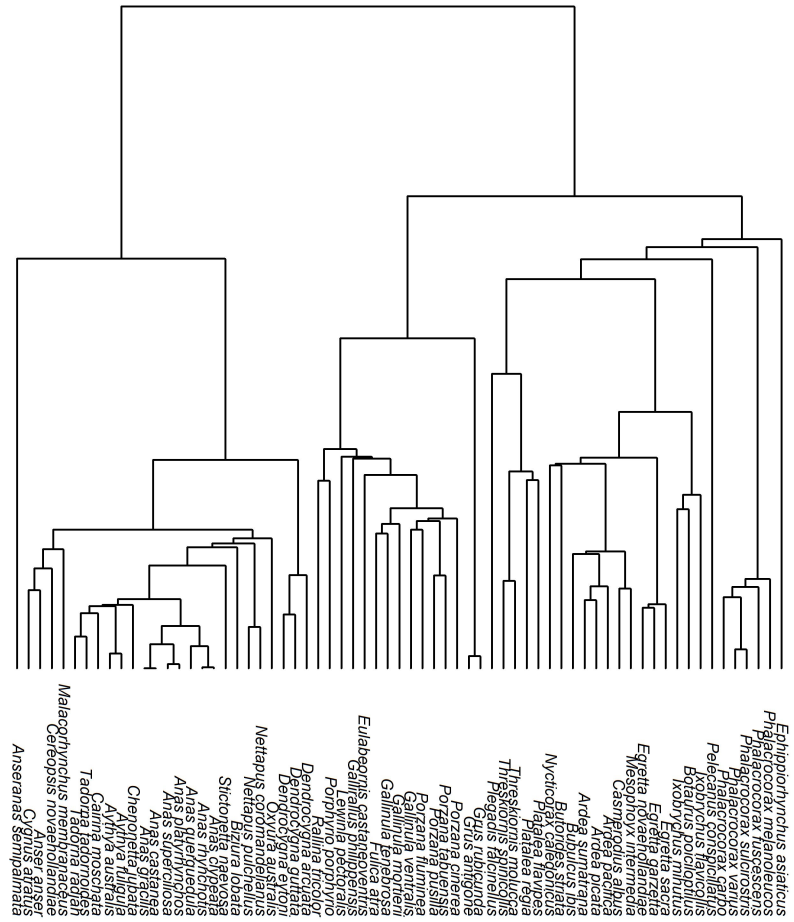
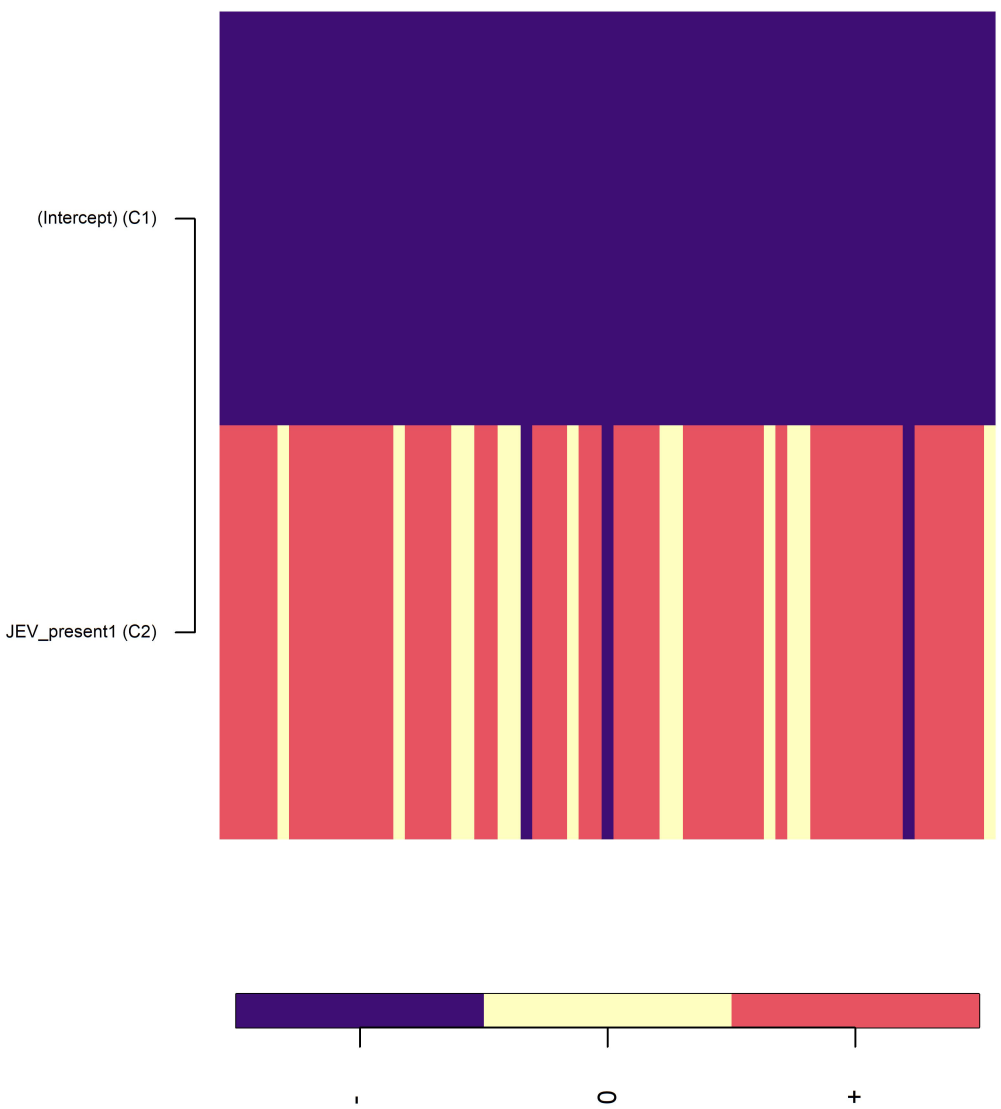
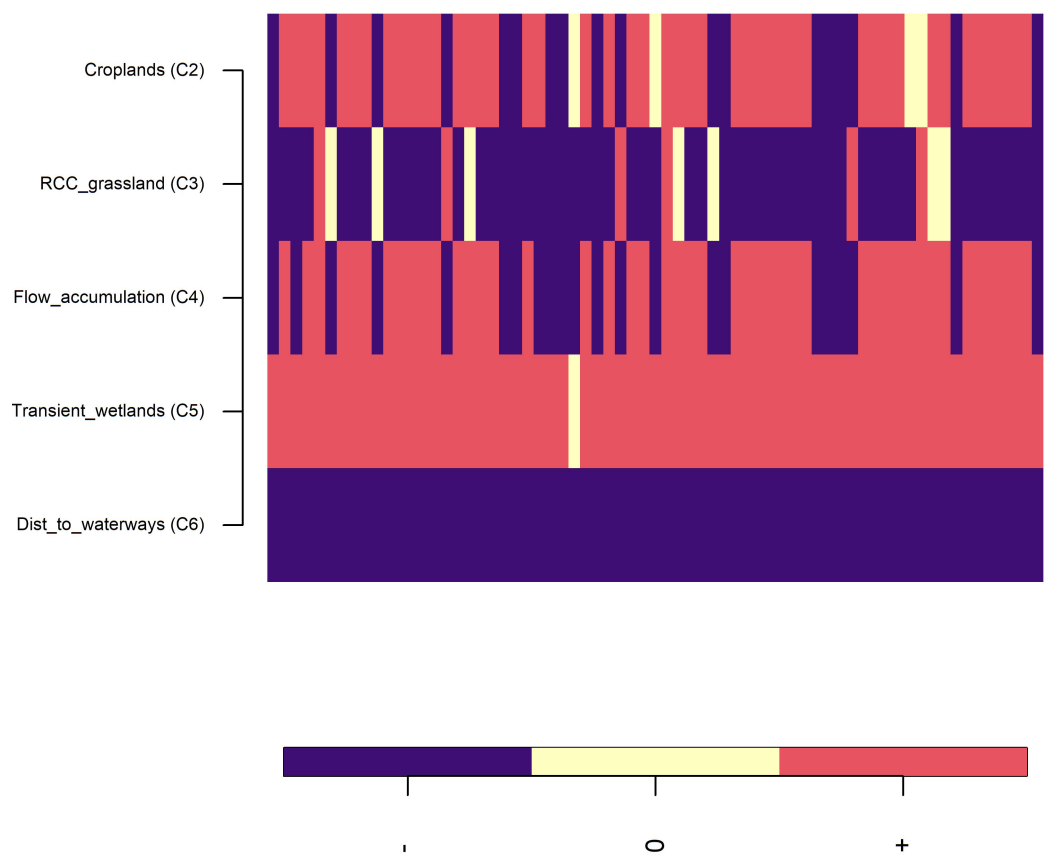
80
60
40
20
0

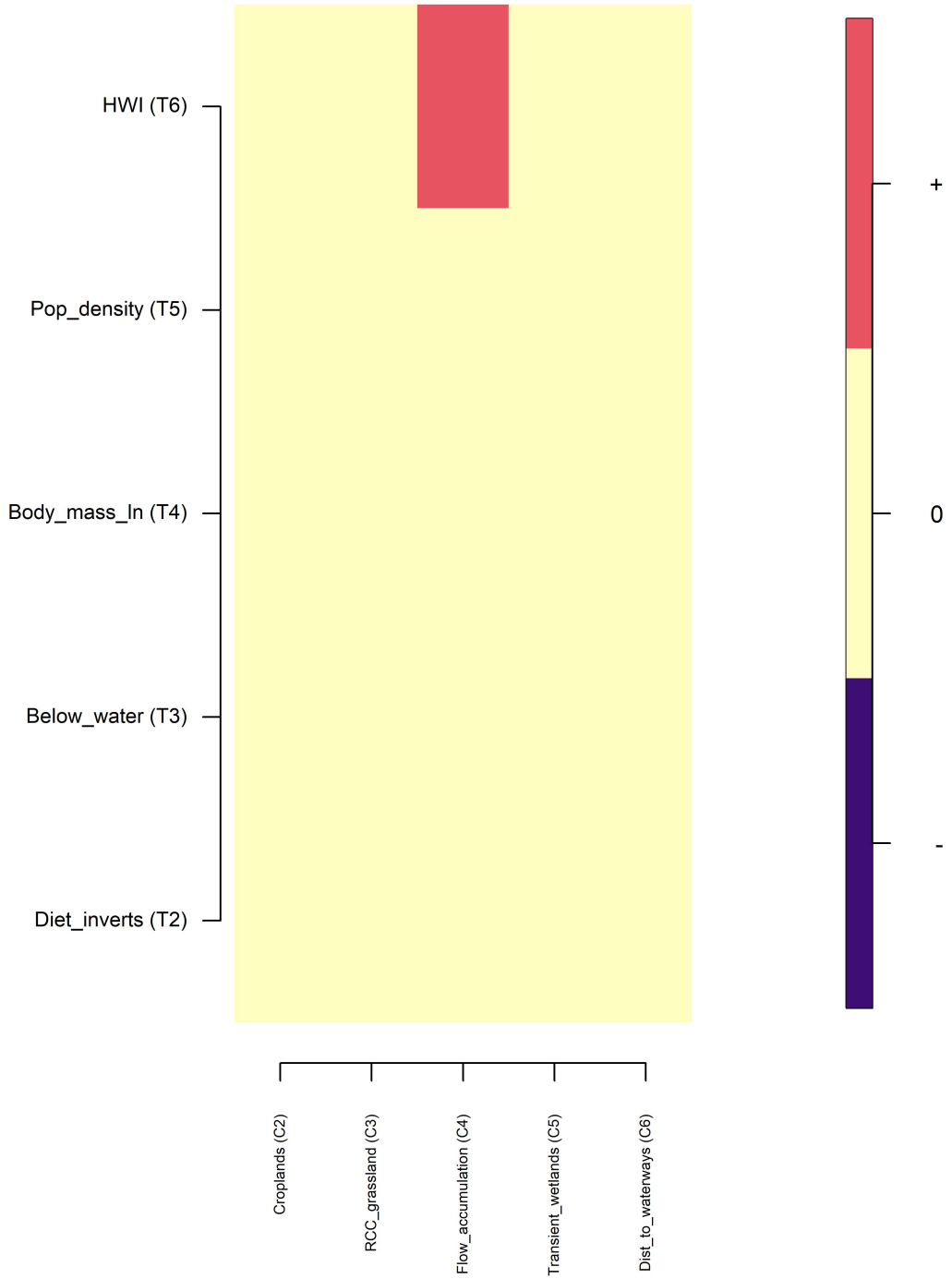

Lower 95% C.L.
Species pool landscape targets (Model 1)
Upper 95% C.L.
Lower 95% C.L.
Species pool landscape targets (Model 2)
Upper 95% C.L.
-10
-15
-20
-25
-30
-35
130
135
140
145
150
155
160
10
8
6
4
2

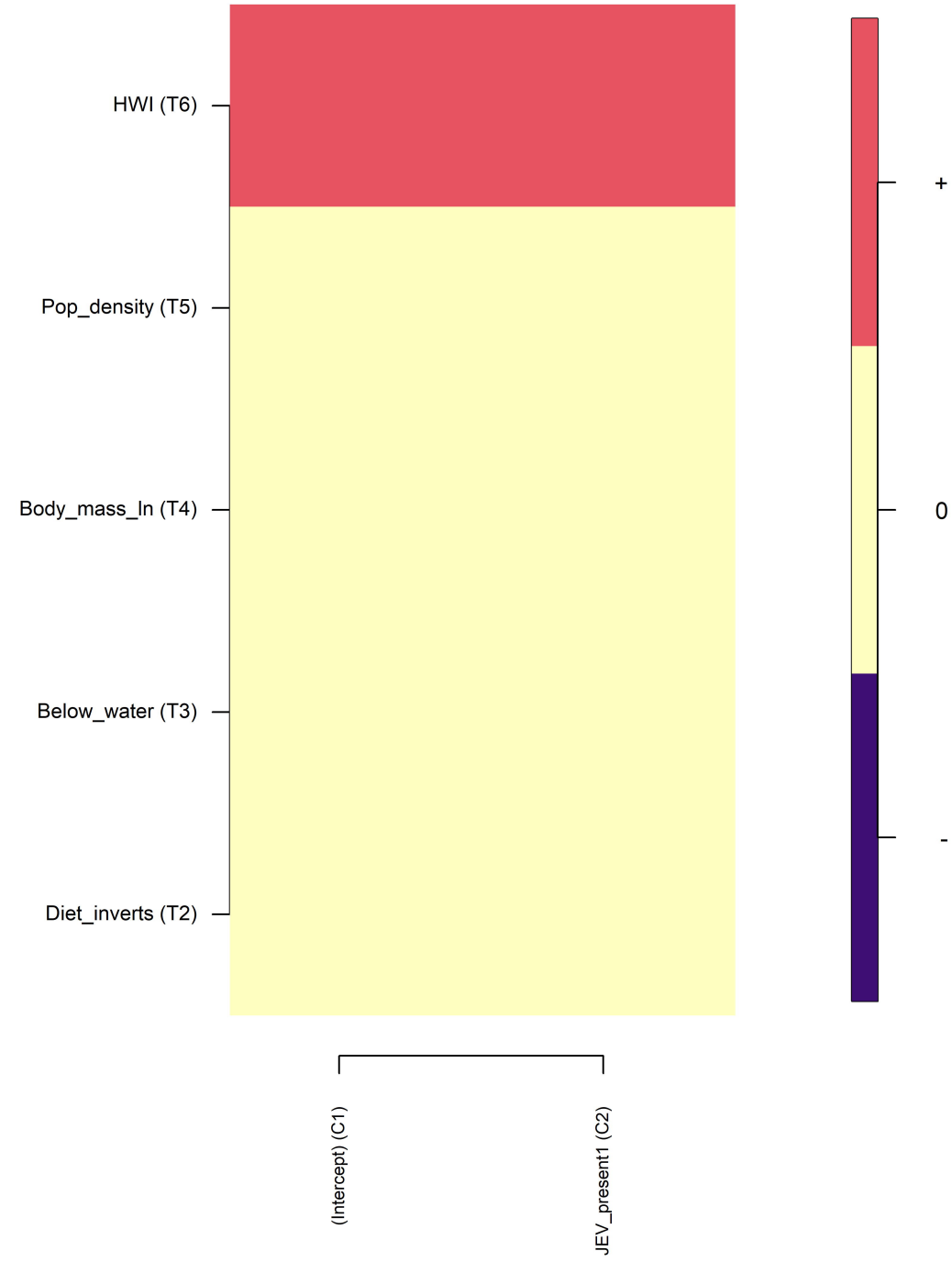

Ephippiorhynchus asiaticus
Phalacrocorax melanoleucos
Phalacrocorax fuscescens
Phalacrocorax sulcirostris
Phalacrocorax varius
Phalacrocorax carbo
Pelecanus conspicillatus
Ixobrychus flavicollis
Botaurus poiciloptilus
Ixobrychus minutus
Egretta sacra
Egretta garzetta
Egretta novaehollandiae
Mesophoyx intermedia
Casmerodius albus
Ardea pacifica
Ardea picata
Ardea sumatrana
Bubulcus ibis
Butorides striata
Nycticorax caledonicus
Platalea flavipes
Platalea regia
Threskiornis molucca
Threskiornis spinicollis
Plegadis falcinellus
Grus rubicunda
Grus antigone
Porzana cinerea
Porzana fluminea
Porzana tabuensis
Porzana pusilla
Gallinula ventralis
Gallinula mortierii
Gallinula tenebrosa
Fulica atra
Eulabeornis castaneoventris
Gallirallus philippensis
Lewinia pectoralis
Porphyrio porphyrio
Rallina tricolor
Dendrocygna arcuata
Dendrocygna guttata
Dendrocygna eytoni
Oxyura australis
Nettapus coromandelianus
Nettapus pulchellus
Biziura lobata
Stictonetta naevosa
Anas rhynchotis
Anas querquedula
Anas platyrhynchos
Anas superciliosa
Anas castanea
Anas gracilis
Chenonetta jubata
Aythya fuligula
Aythya australis
Cairina moschata
Tadorna tadornoides
Tadorna radjah
Malacorhynchus membranaceus
Cereopsis novaehollandiae
Anser anser
Cygnus atratus
Anseranas semipalmata

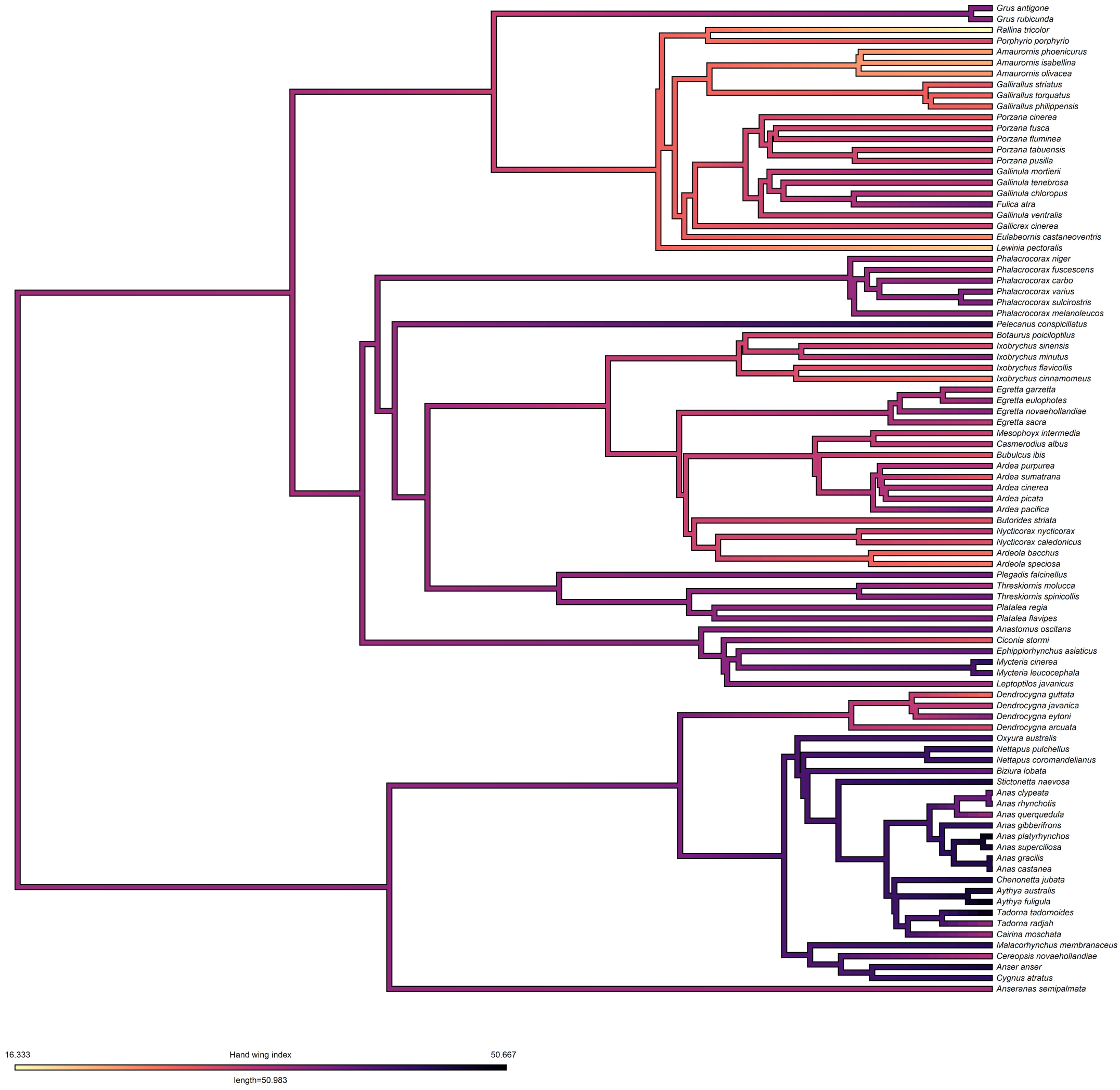

Ephippiorhynchus asiaticus
Phalacrocorax melanoleucos
Phalacrocorax fuscescens
Phalacrocorax sulcirostris
Phalacrocorax varius
Phalacrocorax carbo
Pelecanus conspicillatus
Ixobrychus flavicollis
Botaurus poiciloptilus
Ixobrychus minutus
Egretta sacra
Egretta garzetta
Egretta novaehollandiae
Mesophoyx intermedia
Casmerodius albus
Ardea pacifica
Ardea picata
Ardea sumatrana
Bubulcus ibis
Butorides striata
Nycticorax caledonicus
Platalea flavipes
Platalea regia
Threskiornis molucca
Threskiornis spinicollis
Plegadis falcinellus
Grus rubicunda
Grus antigone
Porzana cinerea
Porzana fluminea
Porzana tabuensis
Porzana pusilla
Gallinula ventralis
Gallinula mortierii
Gallinula tenebrosa
Fulica atra
Eulabeornis castaneoventris
Gallirallus philippensis
Lewinia pectoralis
Porphyrio porphyrio
Rallina tricolor
Dendrocygna arcuata
Dendrocygna guttata
Dendrocygna eytoni
Oxyura australis
Nettapus coromandelianus
Nettapus pulchellus
Biziura lobata
Stictonetta naevosa
Anas rhynchotis
Anas querquedula
Anas platyrhynchos
Anas superciliosa
Anas castanea
Anas gracilis
Chenonetta jubata
Aythya fuligula
Aythya australis
Cairina moschata
Tadorna tadornoides
Tadorna radjah
Malacorhynchus membranaceus
Cereopsis novaehollandiae
Anser anser
Cygnus atratus
Anseranas semipalmata


(Intercept) (C1)
JEV_present1 (C2)
-
0
+


Croplands (C2)
RCC_grassland (C3)
Flow_accumulation (C4)
Transient_wetlands (C5)
Dist_to_waterways (C6)
-
0
+


HWI (T6)
Pop_density (T5)
Body_mass_ln (T4)
Below_water (T3)
Diet_inverts (T2)
Croplands (C2)
RCC_grassland (C3)
Flow_accumulation (C4)
Transient_wetlands (C5)
Dist_to_waterways (C6)
+
0
-


HWI (T6)
Pop_density (T5)
Body_mass_ln (T4)
Below_water (T3)
Diet_inverts (T2)
(Intercept) (C1)
JEV_present1 (C2)
+
0
-


Grus antigone
Grus rubicunda
Rallina tricolor
Porphyrio porphyrio
Amaurornis phoenicurus
Amaurornis isabellina
Amaurornis olivacea
Gallirallus striatus
Gallirallus torquatus
Gallirallus philippensis
Porzana cinerea
Porzana fusca
Porzana fluminea
Porzana tabuensis
Porzana pusilla
Gallinula mortierii
Gallinula tenebrosa
Gallinula chloropus
Fulica atra
Gallinula ventralis
Gallicrex cinerea
Eulabeornis castaneoventris
Lewinia pectoralis
Phalacrocorax niger
Phalacrocorax fuscescens
Phalacrocorax carbo
Phalacrocorax varius
Phalacrocorax sulcirostris
Phalacrocorax melanoleucos
Pelecanus conspicillatus
Botaurus poiciloptilus
Ixobrychus sinensis
Ixobrychus minutus
Ixobrychus flavicollis
Ixobrychus cinnamomeus
Egretta garzetta
Egretta eulophotes
Egretta novaehollandiae
Egretta sacra
Mesophoyx intermedia
Casmerodius albus
Bubulcus ibis
Ardea purpurea
Ardea sumatrana
Ardea cinerea
Ardea picata
Ardea pacifica
Butorides striata
Nycticorax nycticorax
Nycticorax caledonicus
Ardeola bacchus
Ardeola speciosa
Plegadis falcinellus
Threskiornis molucca
Threskiornis spinicollis
Platalea regia
Platalea flavipes
Anastomus oscitans
Ciconia stormi
Ephippiorhynchus asiaticus
Mycteria cinerea
Mycteria leucocephala
Leptoptilos javanicus
Dendrocygna guttata
Dendrocygna javanica
Dendrocygna eytoni
Dendrocygna arcuata
Oxyura australis
Nettapus pulchellus
Nettapus coromandelianus
Biziura lobata
Stictonetta naevosa
Anas clypeata
Anas rhynchotis
Anas querquedula
Anas gibberifrons
Anas platyrhynchos
Anas superciliosa
Anas gracilis
Anas castanea
Chenonetta jubata
Aythya australis
Aythya fuligula
Tadorna tadornoides
Tadorna radjah
Cairina moschata
Malacorhynchus membranaceus
Cereopsis novaehollandiae
Anser anser
Cygnus atratus
Anseranas semipalmata
16.333
Hand wing index
50.667
length=50.983