
SEABIRD ASSEMBLAGES ARE LINKED TO THE MAJOR WESTERN BOUNDARY CURRENT OFF EASTERN AUSTRALIA

SEABIRD ASSEMBLAGES OFF EASTERN AUSTRALIA

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Abstract

Aim: To identify assemblages of seabird species and relate them to environmental conditions off eastern Australia, a world seabird hotspot. **Location:** East coast of Australia. **Methods:** We used 15 seabird at-sea ship-based survey data sets collected over 37° of latitude, from 2016 to 2021, and fitted Region of Common Profile (RCP) mixture models for each season and type of data (presence-absence and abundance). RCP groups are defined as a set of regions where the probability of encountering a specific species profile is constant within regions, but different amongst them. These groups also vary according to covariates, which in our

case included oceanographic, climatic, and physiographic parameters. **Results:** Based on 142,646 seabirds recorded, from 80 species, all models suggested two macro-scale assemblages ('northern' and 'southern'), except for the autumn presence-absence model that identified three groups. The model results consistently show a biogeographic transition at $\sim 34^{\circ}\text{S}$, near the latitude at which the East Australian Current separates from the Australian continental slope. Sea surface temperatures or sea surface salinities were selected in all final models, further indicating a close relationship between seabird assemblages and water masses. Results from both data types, presence-absence and abundance, resulted in similar spatial and species profile patterns. **Main conclusions:** RCP models clearly identified two seabird assemblages off the east coast of Australia, suggesting the persistence of these groups at seasonal and macro spatial scales. Given the rapid climatic changes that the East Australian Current is experiencing and its importance in influencing distributions of seabirds, the methods applied in our study could be replicated to assess possible changes in seabird assemblages, and how they are affected by changing environmental conditions.

Keywords Assemblages · Biogeography · Community ecology · East Australian Current · Mixture models · Region of Common Profiles

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Biosketch

Nicholas W. Daudt (he/him) is broadly interested in spatial ecology and ecological modelling. His research uses data science and modelling to understand biogeographic patterns and ecological processes that build marine top predators' biodiversity patterns across space and time.

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Data availability statement: The gridded data used as the basis for all analyses are available in the archived repository along with the code to reproduce the results. The raw data are currently being used for other projects and thus can not be publicly available. If you are interested in the raw data, please get in touch with Eric J. Woehler.

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Seabird assemblages are linked to the major western boundary current off eastern Australia

Running title: Seabird assemblages off Eastern Australia

Abstract

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Location: East coast of Australia.

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Results: Based on 142,646 seabirds recorded, from 80 species, all models suggested two macro-scale assemblages ('northern' and 'southern'), except for the autumn presence-absence model that identified three groups. The model results consistently show a biogeographic transition at ~34°S, near the latitude at which the East Australian Current separates from the Australian continental slope. Sea surface temperatures or sea surface salinities were selected in all final models, further indicating a close relationship between seabird assemblages and water masses. Results from both data types, presence-absence and abundance, resulted in similar spatial and species profile patterns.

Main conclusions: RCP models clearly identified two seabird assemblages off the east coast of Australia, suggesting the persistence of these groups at seasonal and macro spatial scales. Given the rapid climatic changes that the East Australian Current is experiencing and its importance in influencing distributions of seabirds, the methods applied in our study could be replicated to assess possible changes in seabird assemblages, and how they are affected by changing environmental conditions.

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1 Introduction

Bioregionalization is the discipline that identifies, delimits, characterises, and names biogeographical regions (Morrone, 2018; Vilhena & Antonelli, 2015). Although there is often no agreement on the naming systems among proposed regionalization schema (but see Ebach et al., 2008), the hierarchical nature of bioregions is well recognized (Kreft & Jetz, 2010; Vilhena & Antonelli, 2015). Thus, bioregions are usually described within geographically larger classifications, such as ‘provinces’ or ‘realms’ (Costello et al., 2017; Spalding et al., 2007). The delimitation of bioregions is made through identifying sets of species that are endemic or have high levels of co-occurrence, and are distinct enough from other regions. In this sense, bioregions are interpreted as natural representations of common historical and/or ecological processes shaped by physical and biological forces (Kreft & Jetz, 2010). In particular, the identification of bioregions allows representation of the distribution of multiple species at a given time and space, and relating these regions to environmental characteristics. By doing so, bioregions can be interpreted as species assemblages (N. A. Hill et al., 2017; Lyons et al., 2017). Given these features, bioregions can be used as surrogates for biodiversity monitoring in data-poor regions and in regional conservation planning (Ferrier, 2002; Spalding et al., 2007), playing a fundamental role in conservation biogeography (Whittaker et al., 2005).

Seabird assemblages have been widely described and related to environmental characteristics (Hyrenbach et al., 2007; Ribic et al., 1997; Woehler et al., 2003). Considering the hierarchical nature of oceanographic processes and their resulting features (Haury et al., 1978), it is not surprising that the distribution of highly mobile seabirds are linked differently across temporal and spatial scales (Haury et al., 1978; Hunt & Schneider, 1987). In the marine environment, large scale (>100 km length) oceanographic features (e.g. boundary currents and water masses) act as terrestrial biomes (based on vegetation), and influence seabird assemblage structure—i.e. the occurrence of species and their relative numerical composition (Commins et al., 2014; Hyrenbach et al., 2007; Ribic et al., 1997). In contrast, local abundance is related to meso- (10–100 km) and sub-mesoscale (1–10 km) processes that aggregate prey and therefore predators, such as fronts and eddies (Scales, Miller, Hawkes, et al., 2014; Weimerskirch, 2007). Such processes, although relatively ephemeral, are primarily driven by physical and atmospheric forces, and are thus somewhat predictable in space and time, providing consistent feeding areas for marine predators when they occur (Davoren, 2013; Hazen, Suryan, et al., 2013). Sea surface temperatures are a key driver of seabird distributions, at individual- and assemblage-levels, operating over a range of spatial and temporal scales from macro (e.g. water masses) to fine (e.g. fronts) (Dunlop et al., 1988; Quillfeldt et al., 2015; Ribic et al., 1997). Despite extensive surveys (e.g. Ballance et al., 1997) and tracking studies (e.g. Carneiro et al., 2020), many oceanic regions still lack information on the distributions and abundances of seabird species, and how they assemble in space and time.

One area in need of better understanding of seabird distributions is Australia, considered a global seabird hotspot (Karpouzi et al., 2007; Ramírez et al., 2017). Given the region’s importance for seabird diversity,

there are surprisingly few studies on seabird distributions at sea (Bernard et al., 2021; Mott & Clarke, 2018). Off northwest Australia, at-sea surveys, multivariate analyses (Dunlop et al., 1988) and ensemble species distribution models of species assemblages (Lavers et al., 2014) showed that habitat use by tropical seabird species was related to sea surface temperatures and salinity. Dunlop et al. (1988) suggested that salinity was the main variable influencing species' distributions in oceanic waters while temperature was the key factor for species on the continental shelf. In contrast, there are few studies at large spatial and temporal scales off eastern Australia. T. A. Reid & Hindell (2000) and Evans et al. (2021) analysed seabird assemblages and their relationships with oceanographic and prey data at mesoscale off southeast Tasmania. The remaining studies are mostly descriptive accounts locally (Blaber & Milton, 1994; Norman, 1992), or focused on a single species (Priddel et al., 2014).

The East Australian Current (EAC) is the major western boundary current in the South Pacific Ocean, and the dominant boundary current off eastern Australia (Ganachaud et al., 2014). The EAC has been extensively studied, although the links between the EAC's oceanography and marine predators are not well known. The dynamic features associated with the EAC, such as mesoscale eddies and upwelling, are likely to influence marine biota (Scales, Miller, Hawkes, et al., 2014; Suthers et al., 2011). While most of the biological studies in this system were focused on plankton entrapment within the cores of eddies (Firme et al., 2023; Garcia et al., 2022; Hassler et al., 2011), there is a growing body of work focusing on fisheries (Brieva et al., 2015; Hobday, 2010; Young et al., 2011). These studies emphasized how the probability of occurrence of a given taxon, and the structure of species assemblages, were driven by the EAC. However, the relationships between oceanography and marine megafauna within the EAC are poorly known (Suthers et al., 2011). Some progress has been made using shark and ray movement data (Jaime et al., 2014; Niella et al., 2020; Niella et al., 2022), and satellite tracking has also demonstrated that increased sea surface temperatures in the EAC decreases little penguin *Eudyptula minor* foraging success (Carroll et al., 2016), but information at the assemblage-level for seabirds in the EAC is absent.

Marine species range shifts are more likely to occur faster than terrestrial species due to their higher sensitivity to warming (Lenoir et al., 2020; Pinsky et al., 2019). As a result, climate change is rearranging the structure of species assemblages around the globe (Antão et al., 2020; Dornelas et al., 2014; Poloczanska et al., 2013). Top predators, for instance, may change their core habitats (Hazen, Jorgensen, et al., 2013; Reisinger et al., 2022), with unprecedented population consequences (Woehler & Hobday, 2023). For seabirds, Péron et al. (2010) and Sojitra et al. (2022) showed that sea surface temperature anomalies affected the occurrence and abundances of albatross and petrel species with latitude, thus affecting assemblage structure. In eastern Australia, changing EAC conditions have affected a range of marine species. For example, changes in zooplankton assemblage structure and fish distribution patterns have been recorded and attributed to warming water temperatures, and shifts in shark distributions are expected (C. R. Johnson et al., 2011; Niella et al., 2022). A severe marine heatwave driven by a poleward strengthening of the EAC, showed drastic environmental impacts including

disease outbreaks in aquaculture farms and wildlife mortalities (Oliver et al., 2017). Given that the EAC is strengthening and extending farther southward and getting warmer (Cai et al., 2005; Phillips et al., 2022), biological changes are expected to occur (Hobday, 2010; Poloczanska et al., 2007).

In light of eastern Australia’s importance for seabirds, and the recent attention on how predicted climate change will influence the EAC’s marine biota (Poloczanska et al., 2007), an assessment of the contemporary spatial distributions of seabirds within the EAC at large temporal and spatial scales is timely. Seabirds can serve as sentinels for tracking ecological changes in the EAC in many ways (e.g. Sydeman et al., 2012). Surprisingly though, seabird distribution is under-represented in climate change studies, despite being highlighted as a priority topic (Gr  millet & Boulinier, 2009; Sydeman et al., 2012).

In this study, we aim to identify assemblages of seabird species within the EAC and adjacent areas, and relate these assemblages to environmental conditions, by using at-sea survey data and a state-of-the-art modelling technique. We use the Region of Common Profiles [RCP; Foster et al. (2013)], a mixture model regarded as one of the best available tools for describing bioregions (N. A. Hill et al., 2020; S. N. C. Woolley et al., 2020). RCP is a model-based approach, and has a range of advantages over traditional algorithm-based statistics (N. A. Hill et al., 2020; Warton et al., 2015). Eastern Australia supports a high diversity of seabirds and offers wide environmental gradients over a near 40° latitudinal range, from the tropics to the cool temperate. We hypothesised to find different seabird assemblages relating to different environmental conditions within the EAC. In addition, presence-absence and abundance data were used to test if the different numerical resolutions would result in the identification of similar assemblages. This study provides a repeatable framework on which future studies can assess how future changes in the EAC may influence the distribution of seabird assemblages.

2 Methods

2.1 Study area

The EAC originates from the South Equatorial Current (SEC), a tropical nutrient-poor current. When the SEC’s North Caledonian Jet meets the Queensland Plateau (~18°S), it splits into a north-flowing branch towards the Gulf of Papua and a south-flowing branch, which marks the start of the EAC (Ganachaud et al., 2014; Kessler & Cravatte, 2013). The South Caledonian Jet completes the EAC system at ~22°S after encountering the shelf break in the southern portion of the Great Barrier Reef (**Figure 1a**; Kessler & Cravatte (2013); Ganachaud et al. (2014)). The EAC interacts with the bathymetry of the seafloor, giving rise to oceanographic features and processes, such as smaller currents, upwellings, and persistent dynamic eddies (Oke, Roughan, et al., 2019; Oke & Middleton, 2000; Ridgway & Dunn, 2003). The EAC flows polewards and is primarily associated with the shelf break, but at ~32°S it detaches from the shelf and spawns an area of eddy generation that dissipates throughout the western Tasman Sea (Mata et al., 2006; Oke, Roughan, et al.,

2019), the ‘EAC eastern extension’ (Oke, Pilo, et al. (2019); often termed the ‘Tasman Front’). Although most EAC energy is converted into eddies, the EAC still runs southwards following the shelf break towards Tasmania (the ‘EAC southern extension’; **Figure 1a**), carrying eddy-like features as a transient current (Oke, Roughan, et al., 2019).

2.2 Seabird and environmental data sources

Seabird data were gathered aboard *RV Investigator* and *RV Falkor* on 15 voyages, between 2016/17–2020/21, spanning over $\sim 37^\circ$ of latitude (**Figure 1b**; **Table S1**). One or more observers continuously recorded seabirds within a 300 m forward quadrant (eye height 25 m a.s.l) from sunrise to sunset hours while the ship was underway. The species, the numbers of birds, and their behaviours were logged in real time into a ship-based web server. Environmental parameters for atmospheric and oceanographic conditions were logged continuously by automated-ship based sensors, with seabird observations supplementing relevant environmental conditions such as visibility or associations with marine mammals. Individual records received a date/time/geographic coordinate label (multi-species records have the same label but are logged as separate entries for each species). Birds following the vessels were excluded from analyses. Seabird observation protocols followed Raymond et al. (2010), in use around Australia since 1980.

To investigate and predict species’ distributions and relationships with environmental variables, a considered choice of broad-scale climatic and oceanographic covariates is important (Barbet-Massin & Jetz, 2014). We used three physiographic variables and seven oceanographic variables, from which a further three climatic layers were calculated (**Table 1**). These variables are the most frequently used in seabird-environment relationship studies (Tremblay et al., 2009), capturing processes at a range of spatial and temporal scales from macro-scale water-mass properties to prey availability in meso- to submesoscale oceanographic features (Haury et al., 1978; Scales, Miller, Hawkes, et al., 2014; Weimerskirch, 2007).

2.3 Data treatment

Data wrangling, modelling and visualization were done in R 4.2.0 (R Core Team, 2022); the full list of packages can be found in the Supplementary Material. Code and the modelling dataset (see 2.3.2) are available in (**Zenodo repo**).

2.3.1 Environmental layers

The spatial and temporal persistence of oceanographic features such as eddy kinetic energy (‘eke’) and thermal fronts (sea surface temperature gradient: ‘sst_grad’) may influence the movements and distributions of seabirds by offering a higher likelihood of finding food (Scales, Miller, Embling, et al., 2014; Weimerskirch, 2007). Thus, ‘eke’ and ‘sst_grad’ environmental layers were calculated before extracting environmental data for each seabird record. For both ‘eke’ and ‘sst_grad’, we used their original cell spatial resolution

(**Table 1**) and calculations were done layer-by-layer to match seabird data on the finest spatial scale possible. Eddy kinetic energy was calculated as $0.5(u'\bar{s} + v'\bar{s})$, where $u' = u - \bar{u}$ and $v' = v - \bar{v}$ are the surface zonal (latitudinal) and meridian (longitudinal) geostrophic currents, respectively, using a rolling mean of 90 days as \bar{u} and \bar{v} (Sun et al., 2022). The spatial ‘sst_grad’ for each cell was calculated by averaging the maximum value for each neighbouring cell (average neighbourhood maximum), from north-to-south (NS) and west-to-east (WE); then, the magnitude of the gradient was defined as $NS\bar{s} + WE\bar{s}$ (Burrows et al., 2011). In addition, we calculated climatic seasonal average layers for ‘eke’ and ‘sst_grad’ based on the 11-year data for 2011–2021 as a proxy for persistent oceanographic features, and the ‘eke’ standard deviation over the same period (named with the prefix ‘clim_’ in **Table 1**). Seabed slope was calculated using ‘raster::terrain()’ (Hijmans, 2022a), and distance from the coast was calculated through ‘sf::st_distance()’ (Pebesma, 2018) using Australia and Tasmania as the mainland (i.e. ignoring smaller islands). Then, for each seabird record, the most proximate value for each environmental layer (original or calculated) was extracted using built-in functions from ‘raster’ 3.5-21, ‘terra’ 1.6-7, and ‘sf’ 1.0-8 packages (Hijmans, 2022a, 2022b; Pebesma, 2018).

2.3.2 Data

Seabirds are highly mobile animals, and many species migrate and/or disperse during their non-breeding periods (Schreiber & Burger, 2002). Therefore, seasonal differences in species composition were expected (e.g. K. Reid et al., 2023), and in the probabilities of occurrence and in total numbers. Thus, we built separate modelling datasets for each season. We aggregated seabird data by 1° latitude \times 1° longitude grid cells (*c.* 110×110 km) and season (**Figure 1b**), by summing seabirds from the same species. To test if the presence-absence and abundance (raw counts) data would result in similar assemblage patterns, we built two species matrices, where the presence-absence matrix transformed values >1 to 1. To avoid numerical instabilities in the models prompted by unusual or rare species, we kept only species occurring in at least six grids within each season (summer = 12 species; autumn = 21; winter = 20; spring = 33). The associated environmental data of each seabird record were averaged within the same grid cells and seasons, and environmental data were standardised before modelling.

2.4 Statistical modelling

We used the mixture model Region of Common Profiles (RCP) to identify and describe seabird species assemblages. RCP is a one-stage bioregionalization approach, as it identifies bioregions by specifying a statistical model that simultaneously relates response (multi-species data) and predictor (environmental data) (N. A. Hill et al., 2020; S. N. C. Woolley et al., 2020). Given a set of environmental variables, the model can predict assemblage probabilities for sites where no biotic (observational) data exist. As a model-based approach, RCPs can be compared by information criteria, present uncertainty around the results, and check for model assumptions through assessing distribution of residuals (N. A. Hill et al., 2020; Warton et al., 2015).

The model is specified in terms of assemblages and site-specific probabilities. There are K assemblages (i.e. RCPs), $K = (1, \dots, k)$, that are common across the study area. The outcome variable is a vector $y_i = (y_{i1}, \dots, y_{iS})$, that gives the count or presence-absence of each of the S species at site i . Depending on whether we model the counts or presence-absence data, the assemblages are defined in terms of the expected frequency or relative frequency of the species, respectively. An output of the model is the estimated probability that site i has each of the K possible assemblages. RCPs are a multivariate adaptation of a mixture-of-experts model; as such, the mixing proportions (assemblage structure) vary according to covariates (predictors) (Foster et al., 2013). However, the final estimated assemblage structure is assumed to be constant for all sites belonging to the K assemblages (Foster et al., 2013). As such, RCPs can be directly interpreted as assemblages, and their species profiles as the assemblage structure.

Before fitting models, covariates were checked for collinearity within each seasonal dataset. If a pairwise collinearity of $|x| > 0.7$ was found we removed one of the variables (Dormann et al., 2013), favouring direct measures over the ‘climatic’ layers we calculated (e.g. if ‘sst_grad’ and ‘clim_sst_grad’ were correlated, we chose ‘sst_grad’). Thus, ‘full models’ differed between seasons as the retained covariates varied, although most covariates were common for all seasons.

Due to seabird migration and dispersion, seasons could act as ‘sampling artifacts’ (Foster et al., 2017), thus biasing results (Ponti & Sannolo, 2023). In light of the difference among seasons in the numbers of species that met our occurrence threshold (see 2.3.2), we decided to use RCP models by season and data type (presence-absence and abundance). RCP models were used to relate the response variables (i.e. presence-absence or abundance of each seabird species in each grid cell) to the independent predictor covariates (i.e. averaged values of environmental variables in each cell). Presence-absence data were modelled based on a Bernoulli model, whereas abundance data were based on a Negative Binomial model. RCPs were fitted using the ‘ecomix’ 1.0.0 package (S. Woolley et al., 2022), with the following workflow: (i) find the best number of groups (K) that describes the data, (ii) re-fit the model by fixing K and selecting the optimal combination of covariates, (iii) check residuals, (iv) bootstrap the best model to estimate uncertainty around parameter estimates, and (v) produce results.

To identify the best number of RCP groups (K) that described the data, we used full models (all covariates) with 100 random start numbers (see Foster et al., 2013) between $k = (2, \dots, 7)$ groups, and chose the number of RCPs that minimized the Bayesian Information Criterion (BIC). Then, we fixed K at the optimal number and fitted models for every possible linear, additive combination of covariates. We chose the best model as the one with the lowest BIC. Visual inspection of randomized quantile residual plots modified for mixture models was used to verify model assumptions (Dunstan et al., 2013). To obtain estimates of uncertainty for model parameters (confidence intervals), we used the default settings of ‘ecomix::regional_mix.bootstrap()’, which applies a Bayesian bootstrap 1000 times. A custom code was written to generate partial plots for exploring the influence of covariates on RCP membership.

We built a seasonal 11-year (2011–2021) average layer for predicting model results for each environmental covariate. These variables were then averaged within 1° latitude \times 1° longitude grid cells, by season, between $9-47^\circ\text{S}$ and $141-161^\circ\text{E}$. Note that ‘clim_eke_mean’ and ‘clim_sst_grad’ were processed beforehand as they may characterise persistent oceanographic features (described above) and thus represent the same value as ‘eke’ and ‘sst_grad’. Data for prediction were standardised using the same mean and standard deviation from the modelling dataset.

Finally, we ran rarefaction curves based on the presence-absence matrix and the assigned RCP group for each sample (grid cell) to assess if the amount of information in the RCP model was representative. Rarefaction curves were fit using the ‘iNEXT’ 3.0.0 package (Chao et al., 2014; Hsieh et al., 2016), and results are presented based on alpha diversity (i.e. species richness).

3 Results

3.1 Summary of species richness and numbers

A total of 10,261 seabird records was obtained during the 15 voyages, comprising 142,646 individuals from 80 species, belonging to 11 families and five orders. The five most abundant species made up 83% of total birds counted (43.0% short-tailed shearwater *Ardenna tenuirostris*, 17.2% fairy prion *Pachyptila turtur*, 14.3% wedge-tailed shearwater *Ardenna pacifica*, 5.2% sooty tern *Onychoprion fuscatus*, 3.2% shy albatross *Thalassarche cauta*). The five most frequently encountered species were *A. pacifica* (frequency of occurrence = 35.3%), *T. cauta* (33.2%), brown booby *Sula leucogaster* (25.4%), red-footed booby *S. sula* (25.4%) and black-browed albatross *T. melanophris* (25%) (**Figure S1**). An increase in species richness towards the south of the study region was clear in all but the winter season (**Figure S2**). Noticeably higher counts were made around Tasmania, possibly due to the ‘colony effect’ and/or the presence of Southern Ocean species (**Figure S2**). However, one cell in the Coral Sea had counts of the same order of magnitude as off Tasmania in summer.

3.2 RCP models

For all models, two RCPs was the optimal number of seabird groups, except for the presence-absence-autumn model, which indicated three RCPs as the best fit (**Figure S3**). The best fitting models generally had one or two covariates selected, although the abundance-autumn model had five covariates (**Table 2**). The best models showed a good fit with no apparent deviations from the assumptions (**Figure S4**). All the best models selected ‘sst’ or ‘sss’, as essential for characterising water masses. The thresholds for defining RCP membership were $18-21^\circ\text{C}$ for ‘sst’ and 35.1 PSU for ‘sss’ (**Figure 2, Figure S5**), similar to the characteristics used to define the EAC. Furthermore, most of the best models selected ‘bat’, suggesting a gradient between ‘coastal’ and ‘oceanic’ taxa based on bathymetry (**Figure S5**). Of particular note, proxies

for persistent oceanographic features that may aggregate food resources (the ‘climatic’ variables) for seabirds were selected only in the autumn and spring abundance models.

Grid point-predictions are the assignment of the RCP with the highest probability value for a given cell. When predicting RCP onto space, patterns of point-predictions suggest a biogeographic transition in seabird species around $\sim 34^{\circ}\text{S}$, with both presence-absence and abundance models pointing to similar results (**Figure 3**). These patterns are further reinforced when looking at the mean probability along with the lower and upper confidence intervals of predictions (**Figure 4, Figure S6**), showing that around $\sim 34^{\circ}\text{S}$, the ‘northern’ RCP tended to have higher probabilities in coastal regions, whereas the ‘southern’ RCP spread northward offshore. The autumn presence-absence model (three RCPs) had a similar broad-scale pattern, although the southern RCP is farther south, and a strong ‘Tasmania/Bass Strait’ assemblage appears (**Figure 3, Figure S6**).

The broad pattern of two large-scale assemblages is reflected in their species compositions. Although there are overlaps among the seabird groups, both presence-absence and abundance models captured typical tropical species in the northern RCP (e.g. boobies *Sula* spp., lesser frigatebird *Fregata ariel*) and typical Southern Ocean species in the southern RCP (e.g. small albatrosses *Thalassarche* spp., fairy prion *P. turtur*) (**Figure 5, Figure S7**). The autumn presence-absence model, which had three RCPs, also showed the characteristic taxa representing the ‘northern’ and ‘southern’ RCPs. However, the intermediate ‘Tasmania/Bass Strait’ assemblage showed a mixture of both groups with shy albatross and Australasian gannet *Morus serrator* prominent with high probabilities of occurrence.

4 Discussion

This study showed that seabird assemblages off eastern Australia were correlated with oceanographic conditions, and that the East Australian Current appeared to be key in structuring seabird distributions at meso- to macro scales (*sensu* Hunt & Schneider, 1987). Our results are based on a multivariate statistical model (N. A. Hill et al., 2020), which brings advantages over classical methods for describing species assemblages. RCP models allow estimating uncertainty around the point probability of a sample (grid cell) belonging to an assemblage, thus representing the fuzziness between bioregion boundaries. These transition zones between bioregions are essential for monitoring biological changes due to environmental changes (Morrone, 2023). As such, the boundary between the two consistently identified bioregions in this study may be a crucial region to monitor in future, given noticeable anomalies in the EAC at this same region (Phillips et al., 2022). Our results draw an important baseline for seabird assemblages in a world hotspot for seabirds.

4.1 Seabird bioregions off eastern Australia

The relationships between seabird assemblages and water masses has been known for a long time (Elphick & Hunt, 1993; Pocklington, 1979; Ribic et al., 1997). Thus, it is not surprising that two seabird assemblages were identified off eastern Australia. However, the spatial consistency of these patterns throughout seasons is surprising and remarkable. Resident species seem to characterise these assemblages. Shy albatross (Hedd et al., 2001; Mason et al., 2018) and fairy prions (Fromant et al., 2022) in the southern assemblage, and boobies (Bunce, 2015; Miller et al., 2018) and wedge-tailed shearwaters (McDuie et al., 2015; Weimerskirch et al., 2020) in the northern assemblage, were always profiled with higher probabilities of occurrence and predicted abundances compared to other species in the same groups. Given that changes in assemblages over time are typically driven by a few species (Gotelli et al., 2022), and that those species are likely residents (Souza & Santos, 2023), the relationships between these resident seabirds and the EAC system over the broad latitudinal range detailed here should be closely monitored. Elsewhere, coastal seabirds such as little penguin are signalling the adverse effects that climate change might have in changing seabird behaviours and decreasing foraging success (Carroll et al., 2016; Woehler & Hobday, 2023), which ultimately influence their breeding success and population dynamics (B. Johnson & Colombelli-Négrel, 2021). Thus, the species profiles and the spatial predictions of assemblages from RCP models could be used as tools for monitoring future seabird responses to the fast-changing EAC.

The seasonal models also captured the influence of migratory species, particularly in the southern assemblage. The summer and autumn models reflected the high abundance of short-tailed shearwater before they depart on their trans-equatorial migration (Carey et al., 2014); the presence of the Australasian gannet was picked up by the autumn and winter models (Ismar et al., 2011); and the white-headed petrel *Pterodroma lessonii* movements during chick-rearing and pre-laying exodus (Taylor et al., 2021) were detected in autumn and spring models, respectively. Given the geographic location of the southern assemblage, however, we believe sub-Antarctic taxa were not well represented in our models due to their low number of occurrences and relative paucity of survey effort to date (**Figure S1**; hence they were removed before modelling). Additional surveys may reveal the seasonal northward pulse of these taxa into the southern assemblage (e.g. albatrosses *Diomedea* spp. and *Phoebastria* spp.), given that more effort translates as higher likelihood of recording these species. In turn, including these taxa in the models could result in a more stable ‘three assemblage pattern’ (as revealed by the autumn presence-absence model) in all but the summer season, when the majority of Antarctic species are breeding (S. Marchant & Higgins, 1990).

Our analyses clearly revealed a ‘northern’ and a ‘southern’ assemblage of seabirds off eastern Australia within the EAC. There is a noticeable link with the EAC dynamics: the boundaries of RCPs occurred at ~34°S, near the average separation latitude (~32°S) of the EAC and its eastward extension into the Tasman Sea (Oke, Roughan, et al., 2019). However, the ‘northern/southern’ assemblage pattern identified herein does

not agree with previously-proposed large-scale regionalizations, such as the pelagic Longhurst Provinces (Longhurst, 2007), the Marine Ecoregions of the World [MEOW; Spalding et al. (2007)], or the Large Marine Ecosystems [LME; Sherman (1994)]. The MEOW schema was based on coastal and shelf biota and was meant to represent habitats to the 200 m isobath, which clearly does not encompass the entirety of seabird habitats. The LME schema is characterised by physiographical, hydrological and productivity data but has a strong focus on practical management of areas and thus there is a political component embedded within it, which does not align with seabird distributions. Longhurst (2007) designated only one biogeochemical province for eastern Australia based on productivity patterns, which may work well at larger (macro) scales, but appears to be oversimplified for the EAC.

The results do agree with the marine biogeographic units proposed by Costello et al. (2017), who identified a boundary at $\sim 34^{\circ}\text{S}$ between their ‘Coral Sea’ and ‘South Australia’ realms. Their approach used 65,000 taxa, from benthic/pelagic and coastal/offshore habitats, thus integrating more complexity of the biogeographic boundaries in the marine environment. Other biological data also suggest ‘northern/southern’ assemblages off eastern Australia, including tuna and billfish [also highly mobile top predators; Reygondeau et al. (2012)], mesopelagic fauna [which includes seabird prey; Sutton et al. (2017)] and deep-sea invertebrates and fish (O’Hara, Williams, Althaus, et al., 2020; O’Hara, Williams, Woolley, et al., 2020). All these studies focused mainly on describing biological assemblages, as opposed to classifying environments. It is worth noting that the Longhurst Provinces approach was updated to include SST, SSS and bathymetry (the same variables retained by our best RCP models) and a temporal component to the classification (Reygondeau et al., 2013). The updated provinces are more similar to the seabird assemblages described here, although still not a perfect match, which could be partially explained because the seabird assemblage in the EAC region includes several long-distance migratory species. Australia’s bioregionalization has a long story of disagreements (Ebach, 2012), however, the inherent link that RCPs develop between environment and biological data can be a strong tool to support marine bioregionalization.

4.2 Fitting RCP models to highly mobile animals

To the best of our knowledge, this is the first study applying RCPs to highly mobile animals such as seabirds. RCP models have been previously applied to plants (Lyons et al., 2017), and relatively sedentary animals, such as macrobenthic organisms (Pantiukhin et al., 2021) and demersal fish (N. A. Hill et al., 2017). Oceanic seabirds can have daily movements of hundreds of kilometres (e.g. McDuire et al., 2015), during which they traverse a variety of habitats and environmental gradients. As such, capturing the distribution of highly mobile species, and their relationships with environmental parameters is not a trivial task, and much harder than for sessile organisms.

While remote tracking studies are advancing our understanding on how individual seabirds use their environment at fine scales (Tremblay et al., 2009), they fail to perceive how species assemblages interact with

the environment and each other. Therefore, using at-sea counts of seabirds is a well established method to capture these relationships (Ainley et al., 2012; Hyrenbach et al., 2007; Woehler et al., 2003). Further, the spatial scales on which assemblages relate to their environment is variable and species-specific (Hunt & Schneider, 1987; Ribic et al., 1997; Scales et al., 2017). Understanding the biology of the studied group is thus essential to set the appropriate scales of analyses. Our choice of 1° latitude \times 1° longitude was mainly determined by data availability reflecting survey effort, and the trade-off between the number of species per grid/season (see also 4.3). Nonetheless, the chosen spatial scale is similar to other seabird distribution analyses conducted elsewhere (Harris et al., 2007; Santora & Veit, 2013; Sojitra et al., 2022). Therefore, for describing seabird assemblages at a macro-scale, the chosen resolution seems to have been a good fit, accords with studies elsewhere, and the resultant models described patterns of seabird species' composition consistent with our current understanding of species' ecologies and life history strategies.

RCP models based on presence-absence and abundance data are able to complement each other. Previous studies using RCPs have opted to use only one type of response data. Lyons et al. (2017), N. A. Hill et al. (2017), and Pantiukhin et al. (2021) all used presence-absence data, whereas Lee et al. (2019) and Receveur et al. (2020) used abundance (count) data. The added information contained in abundance data make them inherently more powerful than binary presence-absence data. However, the use of different data inputs in multivariate biodiversity assessments and assemblage descriptions has shown contrasting patterns at different spatial scales. At larger spatial and temporal scales, presence-absence data describe similar patterns to abundance data (Anderson et al., 2005), as we found. In contrast, at smaller scales, abundance data may highlight local conditions and therefore reveal hidden patterns at coarse to fine scales (Anderson et al., 2005; R. Marchant, 1990; Melo, 2005; Waters, 2008). If combined with ecological knowledge of a particular group, the information contained in both presence-absence and abundance data could be leveraged to better interpret the resulting patterns. For example, seabirds will likely occur in specific water masses or currents (Hunt & Schneider, 1987; Ribic et al., 1997), whereas their abundance is related to coarse- to fine-scale processes that enhance prey availability (Hunt & Schneider, 1987; Weimerskirch, 2007). Future studies assessing bioregions of highly mobile animals could describe the compositions of assemblages using smaller resolution grid cells and presence-absence models. Then, abundance models using higher resolution grid cells could improve our understanding of how these animals relate to their environment and possibly reveal multi-species aggregation areas (therefore 'new bioregions') likely nested within the bioregions described at large scales. Such a hierarchical approach would require substantial concurrent observational and environmental data sets, which we suspect do not exist at present.

4.3 Limitations

Although the results suggest consistent patterns, there are a number of caveats to our analyses. Seabird data were gathered during multi-disciplinary cruises, whose sampling designs were not specifically planned to

account for spatial ecology of seabirds. As a result, there are spatial discontinuities in the data, which might have limited the ability of our models to detect the relationships between the seabird assemblages and the full spectrum of environmental predictors. Even though Australia is a hotspot for seabirds (Karpouzi et al., 2007; Ramírez et al., 2017), there is a paucity of information on seabird distributions in the region (Bernard et al., 2021; Mott & Clarke, 2018). Dedicated seabird surveys would help to advance seabird research in this region, and improve our understanding of the patterns described here. By increasing the amount of data, future studies could set the grid cells at higher resolution, and potentially reveal assemblages at finer spatial and temporal scales. In addition, ideally, we would have had more information within each grid cell by season (our sampling units). Nonetheless, rarefaction curves show that the sample coverage (see Chao & Jost, 2012) was high at the RCP level, although there is room for detecting more species in most of them (**Fig S8**).

5 Conclusions

We applied a robust, repeatable method to assess seabird assemblages off eastern Australia within the EAC for the first time. The models point toward a consistent pattern of a ‘northern’ and a ‘southern’ seabird assemblage, where the spatial division is attributable to the eastward separation of the EAC from the coast, and that SST seems to be the key variable discriminating these groups. The EAC has penetrated poleward over the past half-century (K. L. Hill et al., 2008; Li et al., 2022), a trend which is anticipated to continue into the future (Yang et al., 2016), and extreme weather events such as marine heatwaves to happen more often (Oliver et al., 2018). As such, seabirds will have to respond to these changes (Woehler & Hobday, 2023). Southern Ocean albatrosses off southeast Australia, for instance, have shown ‘early stages of a southward range shift’ due to environmental variability (Sojitra et al., 2022). Resident species such as little penguins and wedge-tailed shearwater change their behaviour and have decreased foraging success when SST is higher (Carroll et al., 2016; Peck et al., 2004). Given that eastern Australia is a biodiversity and numerical hotspot for seabirds, it is imperative to establish a monitoring program allowing the assemblages and species profiles presented here to be used as the baseline for understanding possible effects of a warming ocean on seabird distribution. In particular, the transition zone between assemblages (Morrone, 2023), associated with the eastern extension of the EAC, may be fundamental to effectively monitoring strengthening of the EAC and the subsequent impact on marine biota.

6 References

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817 **Data Accessibility Statement**

818 The gridded data used as the basis for all analyses are available in the archived repository along with the
819 code to reproduce the results. The raw data are currently being used for other projects and thus can not be
820 publicly available. If you are interested in the raw data, please get in touch with XXX.

Tables and Figures

- **TABLE 1.** Environmental data used in the Region of Common Profile models applied to seabird data off eastern Australia, their spatial/temporal resolutions, units, and sources
- **TABLE 2.** Full (a) and best (b) Region of Common Profile Models applied to seabird data off eastern Australia, for both data types used (presence-absence, based on a Bernoulli model; abundance, based on a Negative Binomial model). Refer to Table 1 for the environmental data acronyms
- **FIGURE 1.** Study area showing the main ocean currents (a), and seabird records made by season on top of the 1° latitude \times 1° longitude grid cells (b). In (a), the East Australian Current (EAC) system is highlighted with its acronyms in bold and drawn in blue. The South Equatorial Current (SEC) and its branches, the North Caledonian Jet (NCJ) and South Caledonian Jet (SCJ), are drawn in red. The EAC ‘eastern extension’ is an eddy field (blue shaded area) often called the ‘Tasman Front’, from which the East Auckland Current originates (EAUC, in green). Figure (a) is adapted after Oke, Roughan, et al. (2019); for colour references see the online version
- **FIGURE 2.** Partial plots for the retained covariates in the best spring (a) presence-absence and (b) abundance models. The plot shows the fitted probability of belonging to a Region of Common Profiles (RCP) against the environmental value. All other predictors are held at their mean values. Results for other seasons and models can be found in the Supplementary Material (Figure S5). Refer to Table 1 for the environmental data acronyms
- **FIGURE 3.** Spatialized point predictions (hard-classes) for seabird assemblages (Region of Common Profile; RCP), by season, based on presence-absence (a) and abundance (b) models, off eastern Australia. Each grid was assigned to the RCP group with highest membership probability
- **FIGURE 4.** Predicted probability membership of each seabird assemblage (Region of Common Profiles; RCP) and grid, off eastern Australia, from spring presence-absence (a) and abundance (b) models. The central column, ‘mean’, corresponds to the point prediction and Bayesian boot-strapped, lower and upper confidence intervals (CI), on its sides. Note that, in case of two RCPs, RCP2 probability equals (1 - RCP1 probability). Results for other seasons and models can be found in the Supplementary Material (Figure S6)
- **FIGURE 5.** Species profiles of seabird assemblages (Region of Common Profile; RCP) off eastern Australia in spring. Values are the average and 95% confidence intervals of probability of occurrence (a) and predicted mean abundance (b) for each species, based on 1000 Bayesian bootstraps. Values in (b) were log10-transformed to accommodate the high variation between species. Results for other seasons and models can be found in the Supplementary Material (Figure S7)

Table 1:

Variable	Abbreviation	Units	Spatial.resolution	Temporal.resolution	Source
Sea Surface Temperature	sst	°Celsius	$0.25^{\circ} \times 0.25^{\circ}$	daily	Huang et al. (2021) ^a
Sea Surface Temperature gradient	sst_grad	$\Delta^{\circ}\text{Celsius}$	$0.25^{\circ} \times 0.25^{\circ}$	daily	Derived from Huang et al. (2021) ^a
Sea Surface Salinity	sss	PSU	$0.083^{\circ} \times 0.083^{\circ}$	daily	E.U. Copernicus Marine Service Information ^{bc}
Mixed Layer Depth	mld	m	$0.083^{\circ} \times 0.083^{\circ}$	daily	E.U. Copernicus Marine Service Information ^{bc}
8-day average Chlorophyll-a	chl8	mg/m ³	$0.036^{\circ} \times 0.036^{\circ}$	8-days composite	ERDDAP/NOAA ^d
Log10 8-day average Chlorophyll-a	log10_chl8	$\log_{10}(\text{chl8})$	$0.036^{\circ} \times 0.036^{\circ}$	8-days composite	Derived from ERDDAP/NOAA ^d
Eddy Kinetic Energy	eke	m/s	$0.2^{\circ} \times 0.2^{\circ}$	daily	IMOS/AODN ^e
Climatic mean EKE	clim_eke_mean	mean(m/s)/season/10 years	$0.2^{\circ} \times 0.2^{\circ}$	seasonal climatology	Derived from IMOS/AODN ^e
Climatic standard deviation EKE	clim_eke_sd	sd(m/s)/season/10 years	$0.2^{\circ} \times 0.2^{\circ}$	seasonal climatology	Derived from IMOS/AODN ^e
Climatic mean SSTgrad	clim_sst_grad	mean($\Delta^{\circ}\text{Celsius}$)/season/10 years	$0.25^{\circ} \times 0.25^{\circ}$	seasonal climatology	Derived from Huang et al. (2021) ^a
Bathymetry	bat	m	$0.004^{\circ} \times 0.004^{\circ}$	NA	GEBCO ^f
Slope	slope	degrees (°)	$0.004^{\circ} \times 0.004^{\circ}$	NA	Derived from GEBCO ^f
Distance from coast	dist_coast	km	NA	NA	Calculated in R (see main text)

^a NOAA OISST: (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>);

^b 2011–2019: GLOBAL_MULTIYEAR_PHY_001_030 (<https://doi.org/10.48670/moi-00021>);

^c 2020–2021: GLOBAL_ANALYSIS_FORECAST_PHY_001_024 (<https://doi.org/10.48670/moi-00016>);

^d ERDDAP/NOAA (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chla8day.html>);

^e IMOS/AODN (<https://portal.aodn.org.au/search>), 'OceanCurrent - Gridded sea level anomaly - Delayed mode' data set;

^f GEBCO (https://www.gebco.net/data_and_products/gridded_bathymetry_data/)

Table 2:

Model	Model specification	BIC
Bernoulli		
<i>Summer</i>		
a	bat + slope + eke + sst + sss + mld + sst_grad	332.69
b	bat + sss	319.34
<i>Autumn</i>		
a	bat + slope + eke + chl + sst + sss + mld + sst_grad + clim_sst_grad	1184.29
b	bat + sst	1147.94
<i>Winter</i>		
a	bat + slope + eke + sst + sss + mld + sst_grad + clim_sst_grad	1089.43
b	sst	1062.98
<i>Spring</i>		
a	bat + slope + dist_coast + eke + chl + sst + sss + mld + sst_grad + clim_sst_grad + clim_eke_mean	2345.6
b	bat + sst	2306.7
Negative Binomial		
<i>Summer</i>		
a	bat + slope + eke + sst + sss + mld + sst_grad	1518.96
b	bat + sss	1505.13
<i>Autumn</i>		
a	bat + slope + eke + chl + sst + sss + mld + sst_grad + clim_sst_grad	-Inf (n.f.)
b	bat + chl + sst + mld + clim_sst_grad	3082.14
<i>Winter</i>		
a	bat + slope + eke + sst + sss + mld + sst_grad + clim_sst_grad	3262.45
b	sst	3234.21
<i>Spring</i>		
a	bat + slope + dist_coast + eke + chl + sst + sss + mld + sst_grad + clim_sst_grad + clim_eke_mean	5854.32
b	sst + clim_eke_mean	5824.38

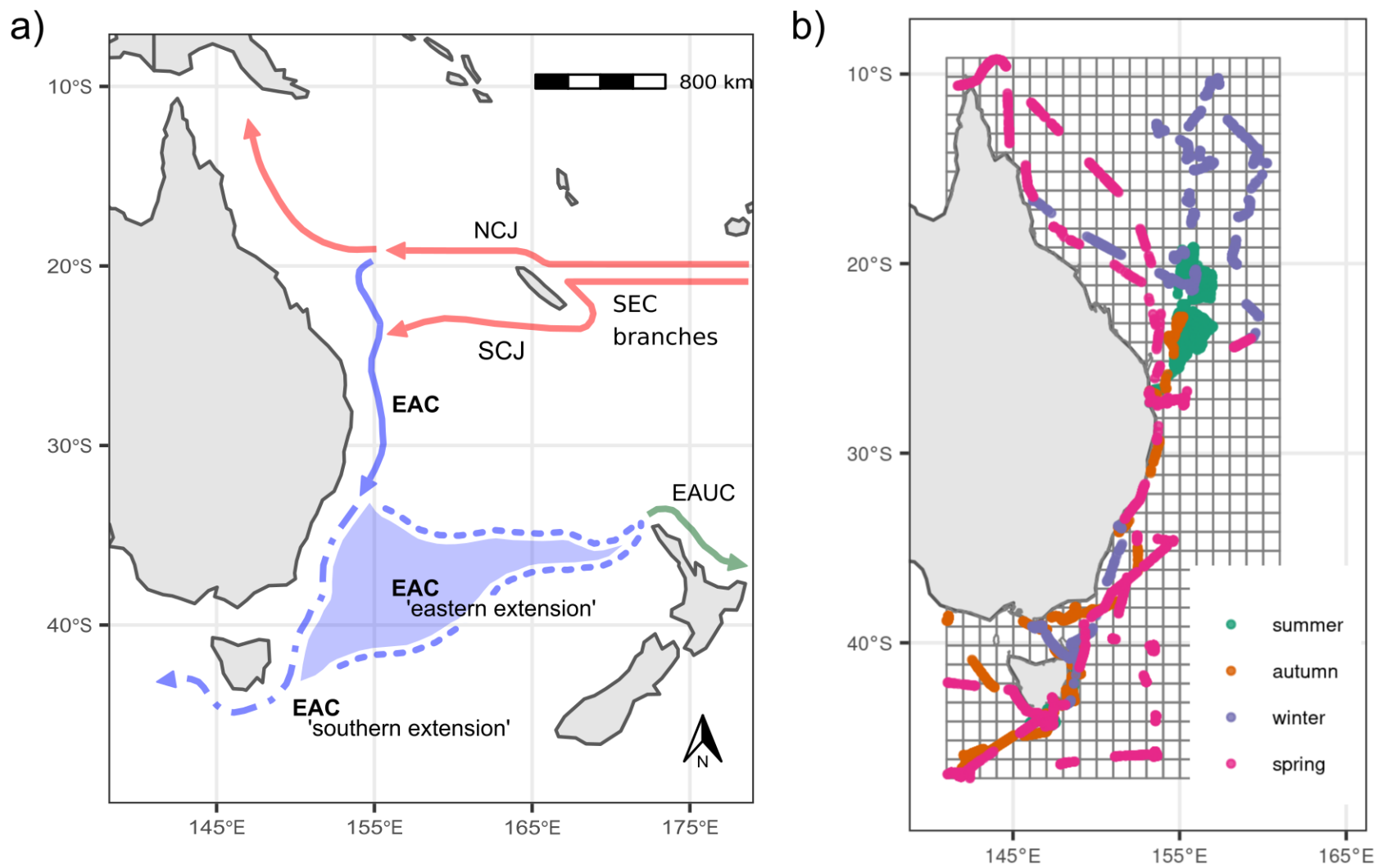
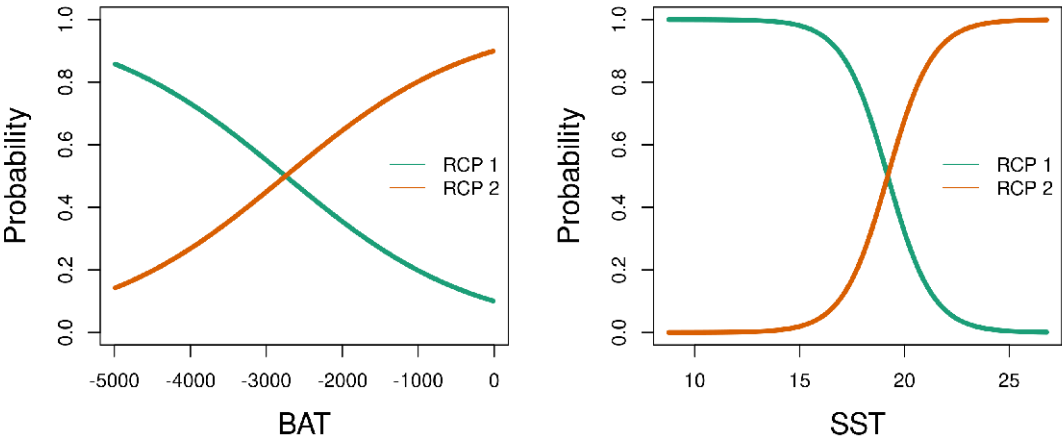


Figure 1:

a)



b)

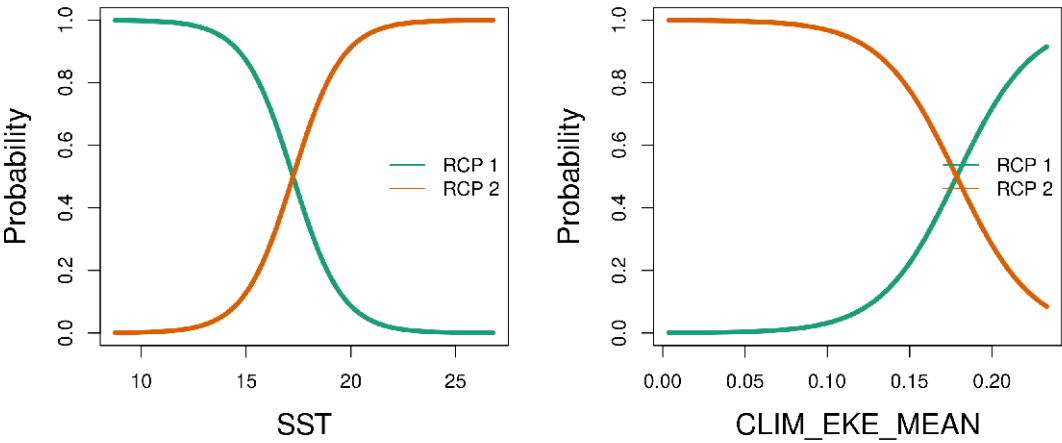
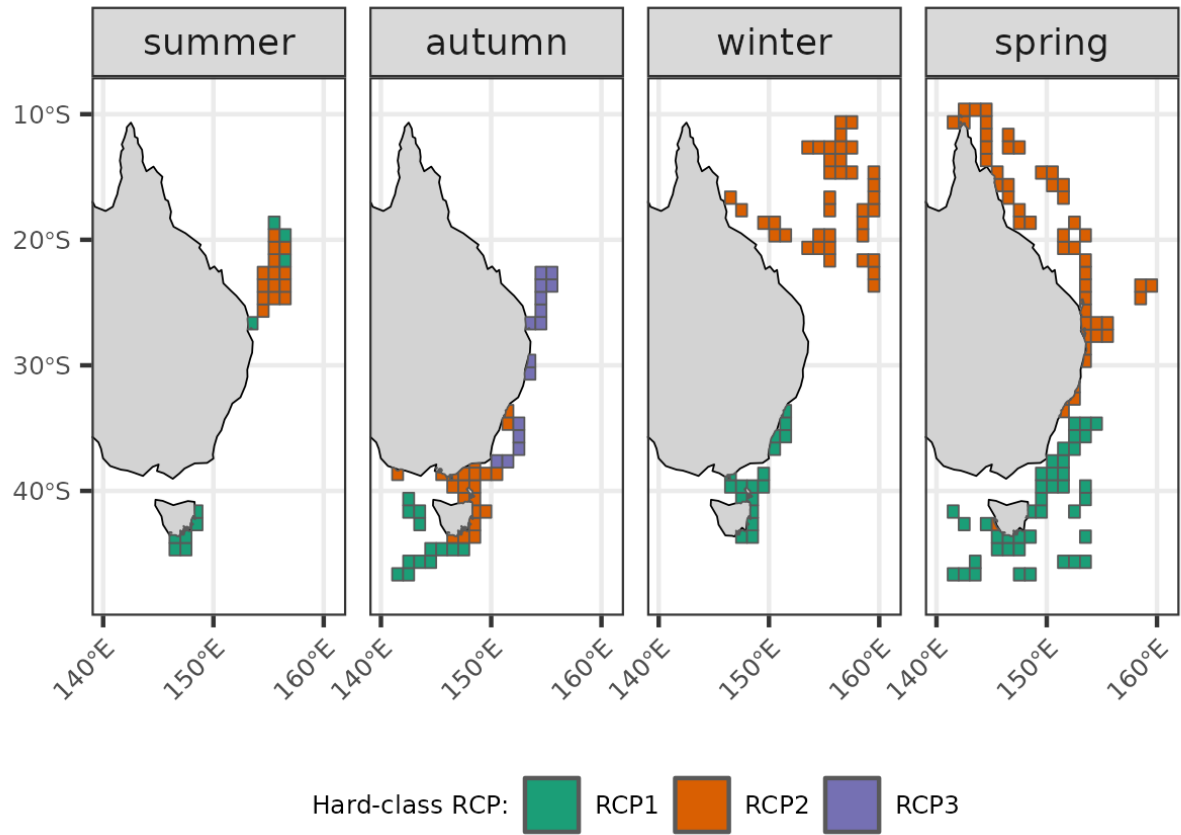
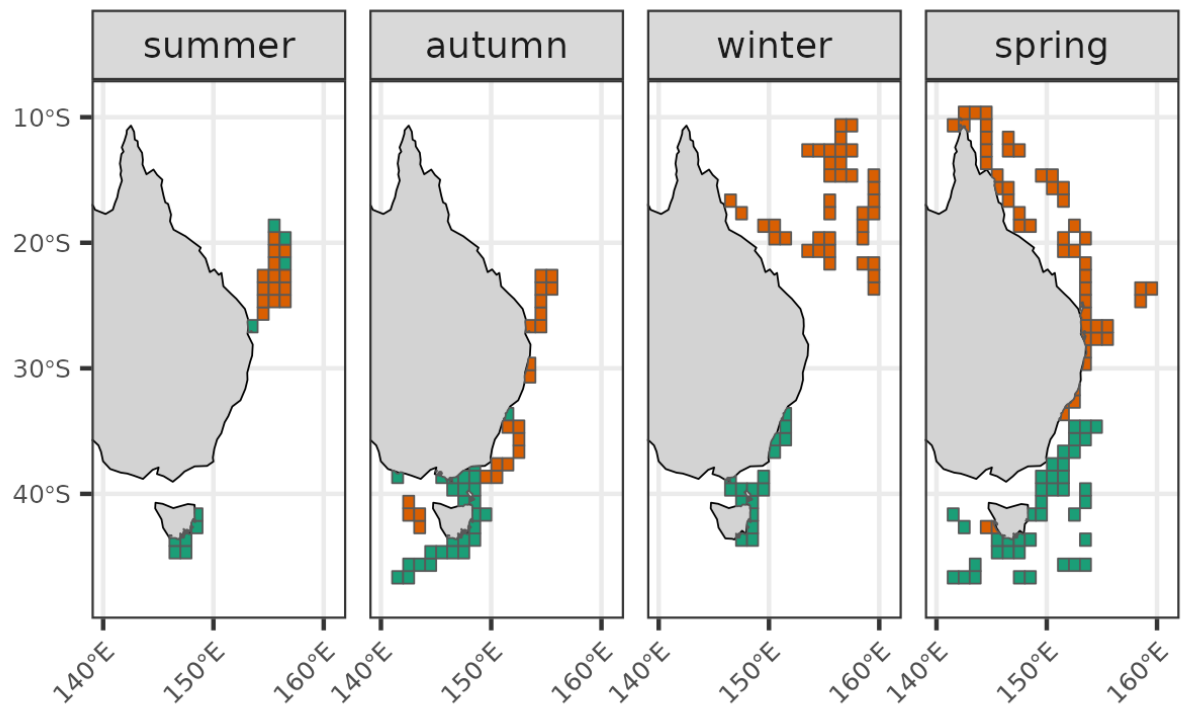


Figure 2:

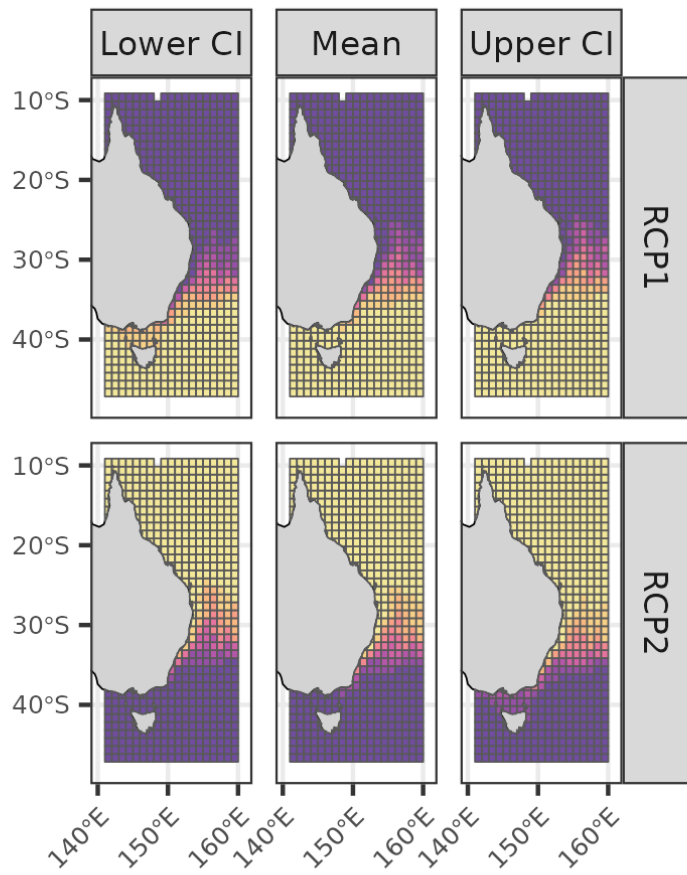
a)



b)



a)



b)

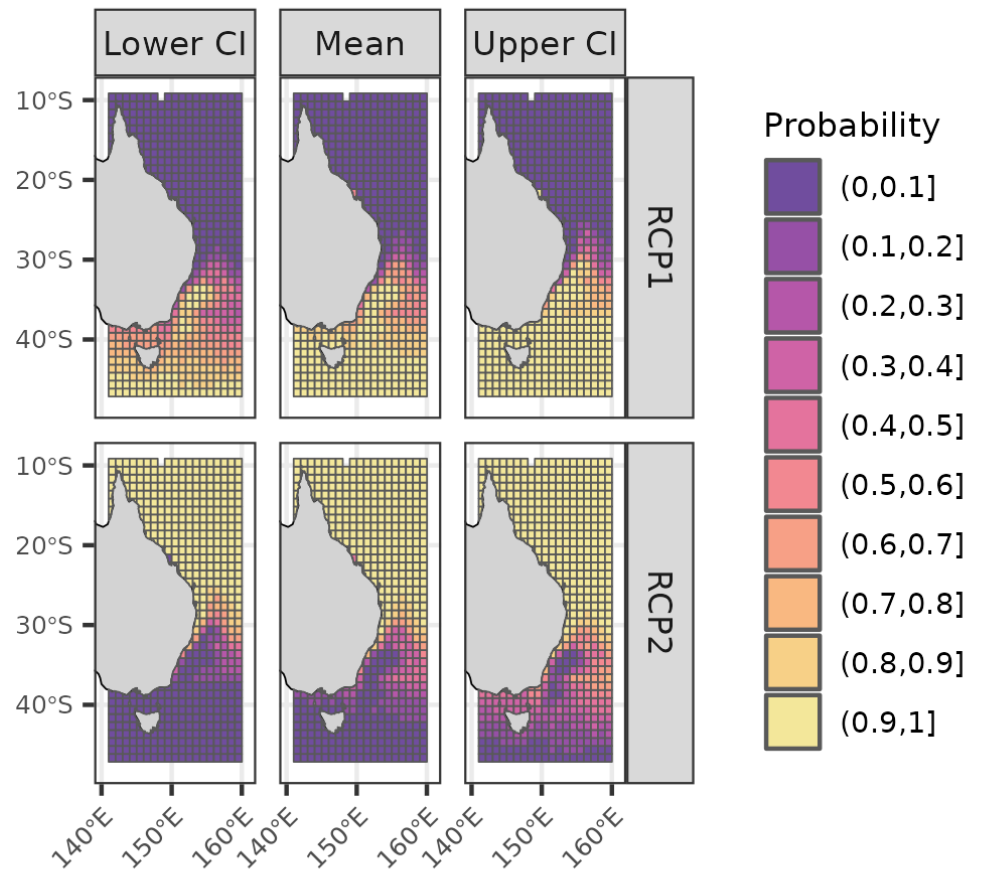
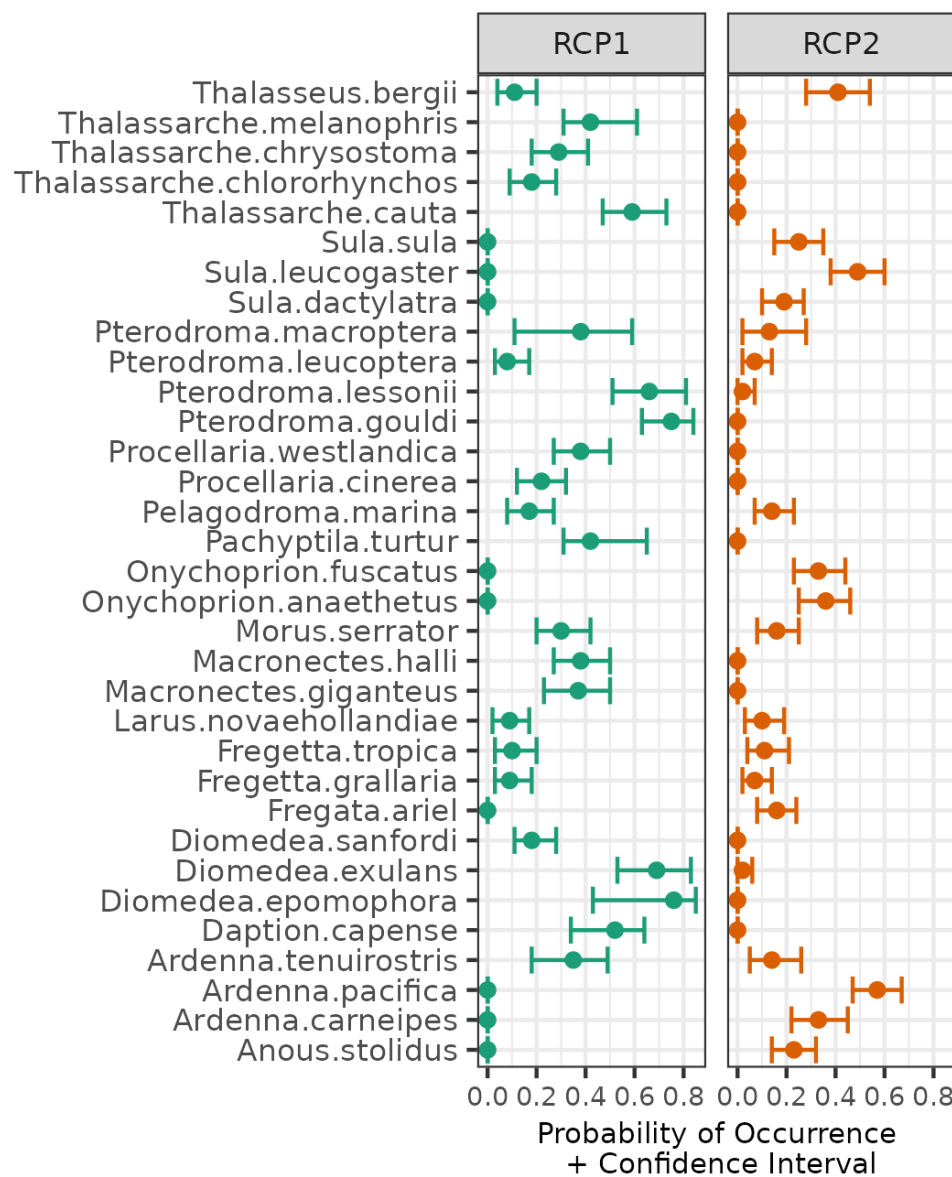


Figure 4:

a)



b)

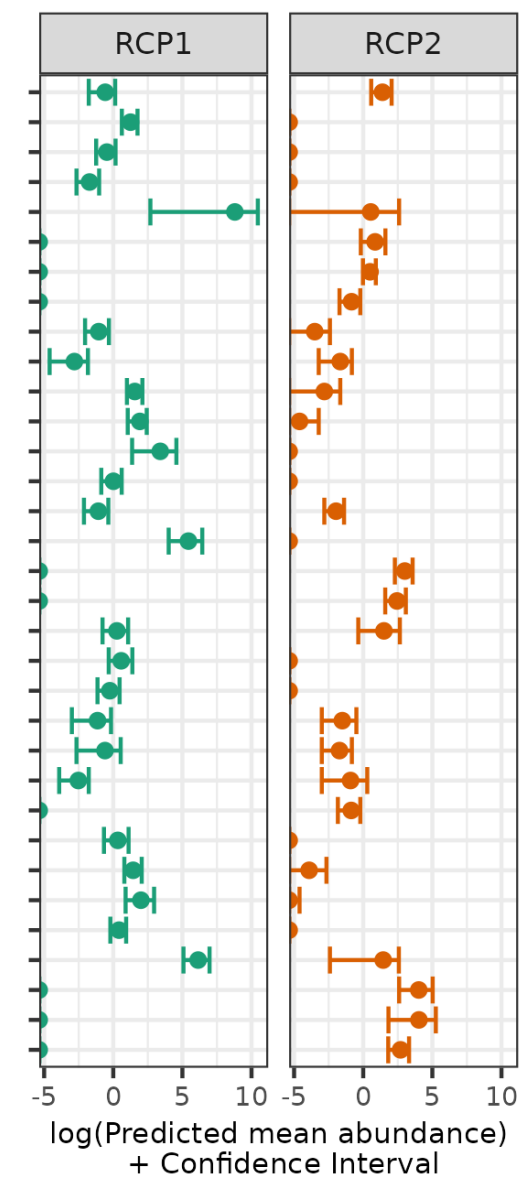


Figure 5: