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Island Plant Species Distributions Contracted at the Cooler Edge Compared to Mainland

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ABSTRACT

Continental islands have long been used as ecological models for understanding species assembly dynamics in isolated habitat fragments. But competition or colonisation constraints might be different to mainland populations, manifesting as expanded or contracted ranges across a geographic distribution of islands in comparison to a mainland population range. Here, we demonstrate that plants on coastal islands do not experience ecological release due to lack of competition, but rather a contracted range at the cool edge in a cross-continental dataset of 843 small coastal islands spanning contrasting environments fringing the Australian coast. We found the cool edge of species ranges across their distribution of small islands averaged 2.2°C warmer in mean annual temperature, or about 4–500 km nearer the equator. The tendency not to colonise islands at the cool edge suggests species may struggle to track their niche poleward as the climate shifts over fragments of habitat on the mainland.

1 | Introduction

Small, continental islands have long been used as model systems for biogeography and landscape ecology. The replicated nature of isolated habitats has provided the opportunity for scientists to study and test theories that can be applied to habitat fragmentation, evolution and species turnover (Hanski 1998; MacArthur and Wilson 1967; Schrader et al. 2021; Warren et al. 2015; Whittaker et al. 2023). A key concept of these theories is that the vegetation community on each island is the result of a filtering process from the mainland source pool. It is well known that the isolation of an island limits the number and type of species that occur on islands. For example, a lack of dispersal specialisation and abiotic pollination syndromes favour certain species reaching oceanic islands (König et al. 2021). There are also practical applications of ecology theory from studying islands. Understanding how and when species inhabit isolated habitats from the Theory of Island Biogeography has guided decisions in the creation of conservation areas and reserves (Whittaker et al. 2023).

When defining species ranges on continental landmasses, the cool and warm edges of temperature ranges are an important environmental variable for defining areas of appropriate habitat (Estrada et al. 2015; Körner et al. 2016; Westoby et al. 2024). Many authors, including Darwin, have hypothesised that warm edge limits of species are more frequently governed by biotic interactions such as competition, predation/herbivory or pathogens, in contrast to cool edge limits that are mainly due to harsh abiotic conditions that limit the fitness of organisms (Cahill et al. 2014; Darwin 1859; Körner et al. 2016; Lyu and Alexander 2022; Paquette and Hargreaves 2021). If this theory were to apply to islands, the warm edges of species ranges might be warmer on islands than on the mainland due to decreased competition and predation (Figure 1B, yellow symbols), that is, species may be able to inhabit islands that are warmer than the upper limits of where they grow on the mainland. This effect of competitive (Segre et al. 2016) or ecological release (Herrmann et al. 2021) has been documented mainly on oceanic islands in both native and non-native

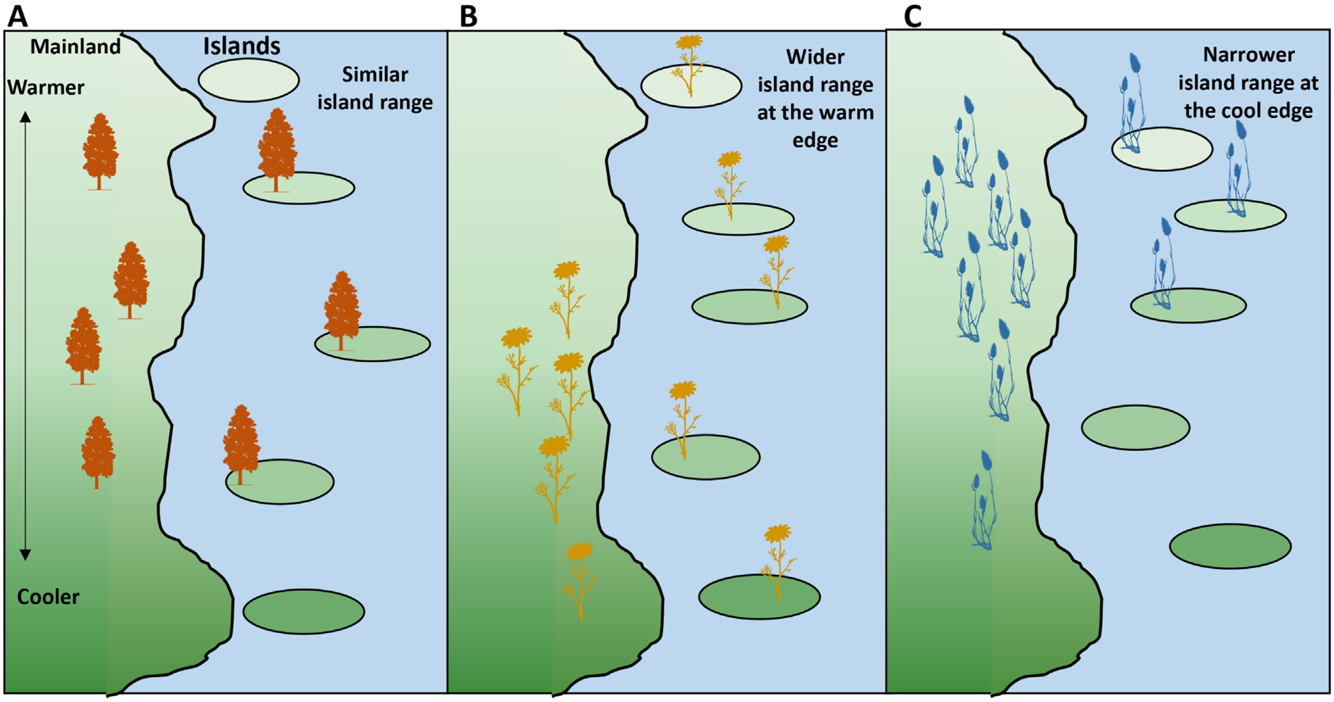

FIGURE 1 | Conceptual diagram of species temperature ranges on the mainland in comparison to islands. Each species has a warm and a cool edge of their range both on the mainland and across a geographic distribution of small islands. (A) A mainland vegetation population spanning a range of temperatures similar to those of a group of islands off the coast. (B) Due to reduced competition on islands, species could inhabit islands that are warmer than their mainland range. (C) Plant species in general may have a narrower species range at the cool edge, which might reflect poorer survivorship or reproductive output at the cooler edge. Silhouettes Keesey, T. Michael, Phylopic, www.phylopic.org, date accessed 2/9/24.

vegetation via mechanisms such as reduced herbivory, disease or competition from other species (Atwood and Meyerson 2011; Barton and Fortunel 2023). Whether or not this effect would also occur on continental islands has not been clearly established.

On the other hand, the cool edge of species ranges might be warmer, causing a contraction of the temperature range for plant species on islands. Following the hypothesis of Darwin and others that the cool edge is governed by harsh abiotic conditions that limit the fitness of organisms, poorer survivorship or reproductive output at the cooler edge of species ranges might decrease the ability of species to reach islands or increase the rate of extinction of small local populations that successfully colonise them (Figure 1C, blue symbols). Other reproductive traits such as dispersal syndromes may be associated with niche fill (Carlquist 1966; Leo et al. 2021; Whittaker et al. 2023); species that disperse by wind or animal vectors might inhabit islands towards the edges of their temperature niche more so than those dispersed by ants or gravity. Alternatively to expanded or contracted ranges on islands, plant species might on average inhabit islands over a similar range of climates to what is observed on the mainland. This can be considered a sort of null hypothesis, whereby biotic factors on islands do not have different effects compared to the mainland (Figure 1A, red symbols). These three scenarios do not exhaust all the possibilities. For example, if boundaries were actually determined by temperature extremes, then buffering of those extremes by the surrounding ocean might confer wider distributions on islands when measured in terms of mean temperatures. Despite the prevalence of ecological release theory in island biogeography (Barton and Fortunel 2023; Segre et al. 2016) and the assumption that species occupy islands with similar climates to the mainland (Benavides Rios et al. 2024; Itescu 2019), few studies have directly tested how temperature as a filter might act in the context of island colonisations. How does filtering of species due to insularity interact with temperature in selection of species that occupy coastal islands? We can answer this question by contrasting the temperature ranges and the warm and cool edges of species ranges across islands and the mainland.

Understanding how temperature interacts with isolated patches of habitat such as coastal islands in limiting species ranges is useful for predicting how species may respond to climate change (Cahill et al. 2014). For example, if the theory of ecological release is confirmed for small coastal islands and species can generally inhabit islands that are warmer than their upper limit on the mainland, this would suggest that plants are able to tolerate warmer conditions that they will experience in the future, that is, competition is limiting species at the warm edge of species ranges on the mainland (Cahill et al. 2014; Paquette and Hargreaves 2021). However, if species fail to inhabit islands over the full range of temperatures on the mainland, this suggests species will generally find tracking their climate niche poleward more difficult as their temperature boundaries shift over patches of habitat and reserves on the mainland (Corlett and Westcott 2013; Neilson et al. 2005; Whittaker et al. 2023).

Here, we test these predictions about differences in species ranges on continental islands versus the mainland across a whole continent. We compare the range of temperatures inhabited by species on islands with their mainland populations, and test for some drivers that might explain differences including geographic (distance to nearest mainland populations) and traits (growth form, dispersal syndrome). Australia is fringed by >8000 islands comprising a range of environments, substrates and plant species composition, extending from the tropics to cool temperate climates (latitudes 9° to 44° South). We sourced species island occurrences from comprehensive flora surveys for more than 840 of these coastal islands that have been collated and standardised in the A-Islands database (Schrader et al. 2025). The mostly small coastal islands in this dataset (95% are $<2\,\mathrm{km}^2$ and $<100\,\mathrm{km}$ from the mainland) span mean annual temperature (MAT) from 12°C to 28°C (Figure S1). We also assembled occurrence records on the mainland for the 1530 species present on more than six islands, to compare the temperature range limits of species on islands to their mainland populations.

2 | Materials and Methods

2.1 | The List of Island Flora

Species occurrence for islands was sourced from the A-Islands database, which is a dataset of flora surveys of Australia's islands. The dataset comprises 58,223 occurrence records for 5920 plant species on 843 islands spanning a time period from 1940 to the present day. The 843 islands include representatives from many different archipelagos and span the whole range of environments of Australia's vast coastline, including monsoonal, tropical, subtropical, temperate and cool temperature, and substrates including sand, coral and rock (Figure S1) (Australian Government Department of Climate Change 2009; Schrader et al. 2025). Only surveys that contain the complete vascular floras of islands are included in the A-Islands database. The fact that these surveys are only those that record the complete flora of an island, in contrast with partial surveys of islands sampling plots or subsections, provided added confidence in determining species distributions on islands (König et al. 2019). We considered an island to be part of the island geographic range of the species if it had been observed there at any time and on any survey. A-Islands only includes Australia's coastal islands, whose flora is maintained by high and constant colonisation and extinction dynamics (Schrader et al. 2023b). Given the relatively few oceanic islands surrounding Australia (6 islands) and their unique and often endemic vegetation communities (Schrader et al. 2024) that contrast with the environments found on coastal islands and the mainland (Supplementary methods), we decided to exclude these locations from the analysis. Species were filtered to only those native to Australia (5304 species) to remove introduced species that may still be in the process of filling their mainland and island temperature range.

Exploratory data analysis revealed the distribution of islands per species to be highly skewed (mean of 10, median of 3), with many species having been observed on only one or two islands (Figure S2). We selected a minimum of six island occurrences per species as a threshold for the subsequent analyses, a number of records listed as above the minimum threshold for island species distribution models (Benavides Rios et al. 2024), to retain as many species as possible from the original dataset while providing a meaningful number of observations from which to calculate the temperature range. This subset of data consisting of species occurring on a minimum of six islands contained 49,480 occurrence records (85%) of 1530 plant species (31%) on 843 islands. To ensure these results were consistent across more stringent thresholds of island occurrence numbers, we also repeated the analysis with only species that occurred on at least 10 islands (1128 species) and at least 20 islands (602 species). These thresholds produced similar results (Figure S2 and Table S1).

2.2 | Species Traits

We used near complete datasets for plant growth form, life history and woodiness for all Australian plants (Wenk et al. 2024) accessed via the AusTraits plant trait database v. 5.0.0 (Falster et al. 2021). There were 36 species that were missing plant growth form, life history or woodiness trait values. These were gap-filled by inferring traits from other known traits in AusTraits (27). For example, if a species was identified as being annual it was inferred to be herbaceous (woodiness trait) and a herb (plant growth form). The remaining species traits were sourced from species descriptions on Plants of The World Online (seven species) (POWO 2024), Useful Tropical Plants (four species) (Theferns 2024) and PlantNET (three species) (PlantNET 2024).

Continuous trait data for maximum plant height, seed dry mass and leaf mass per area (LMA) was also sourced from the AusTraits plant trait database, with the raw observations from many sources aggregated to produce a site-weighted mean value per species. Plant height trait values were supplemented by internet searches similar to categorical traits described earlier. Seed dry mass and LMA values were supplemented by data from the TRY plant database (Kattge et al. 2020) by querying for any species without a trait value. Mean trait values were calculated from this data in a similar way to that described above—the mean of the log transformed values. Seed dry mass values from seedless species (e.g., ferns) were removed, as well as plant height values from species classified as climbers or aquatic plants in AusTraits.

Dispersal syndromes were also assigned to species from the Diaspore dispersal syndrome trait in AusTraits. To better isolate the effect of dispersal syndrome on species occurrence on islands, species with multiple trait values were condensed so as to represent only one single trait value per species using standardised look-up tables for each unique combination of multiple trait values, for example, a species that was described as zoochorous, as well as endozoochorous was simply described as endozoochorous. Species that still possessed multiple dispersal syndromes were removed from the analysis so only species with a clear, dominant dispersal syndrome were included. The 39 hydrochorous species were also excluded from the analysis as the majority were aquatic plants, for example, mangroves, while this work was focused on the terrestrial flora of islands.

2.3 | Island Species Climate Ranges

Various different measures of temperature have been related to species distributions (Körner and Hiltbrunner 2018; Yalcin and Leroux 2017). To define the temperature limits of each plant species, we use primarily Mean Annual Temperature (MAT) of locations where the species is known to occur. MAT is commonly used across many fields in plant ecology, including species distribution models and climate change response studies (Benavides Rios et al. 2024; Gallagher et al. 2019; Hanz et al. 2023), because it is considered a summary variable describing the climate of a location. MAT in this study corresponds to Bioclim Variable 1 published in the Chelsa Bioclim+ dataset (Karger et al. 2017) and is the mean of temperatures in a year for the period 1981–2010.

Other literature also points to extremes of temperature as important in defining extinction events for plant populations and causing the most stressful conditions for plant species (Hatfield and Prueger 2015; Román-Palacios and Wiens 2020). Consequently, we also analysed the mean Maximum Temperature of Warmest Month (MTWM), Bioclim variable 5 and Minimum Temperature of Coldest Month (MTCM), Bioclim variable 6 for the period 1981–2010 in addition to MAT to define the temperature range of species (Karger et al. 2017).

These variables were extracted from the Chelsa Bioclim+ dataset (Karger et al. 2017) for each island's coordinates in the A-Islands database and other mainland occurrence coordinates (described below). The lower end of the range (cool edge) was defined by the minimum MTCM and MAT and the higher end by the maximum MAT and MTWM of islands where species had been observed. Temperature range size (ΔMAT) was the difference between the maximum MAT and minimum MAT of the occurrences for each species.

2.4 | Mainland Species Climate Ranges

In order to access and clean mainland occurrence data for these island species, we followed the method described in Gallagher et al. (2019) with some minor adjustments to suit our analyses. The full method is as follows: to define the mainland climate range, occurrence data for the same 1530 plant species were downloaded from the Atlas of Living Australia online portal. Downloads were carried out using the galah R package (Westgate et al. 2024) with the *atlas_occurrences* function and occurrences filtered to those occurring in Australia and part of the Atlas of living Australia Species Distribution Modelling data profile.

The data were then filtered sequentially through the following conditions so that unwanted observations were removed. Numbers in parentheses record how many observations remained at each step: Data from resources forming part of the Australian Virtual Herbarium (577,197 observations), observations with geographic coordinates (568,854 observations) and with species names matched back to the original queried names following removal of infraspecific epithets such as subspecies, form and variety (562,843). Only one unique record for each combination of species name, latitude, longitude, month and year was retained (557,221). Records coming from a cultivated or garden environment were removed using the *str_detect* function from the *Stringr* package (Wickham and Wickham 2019), which analysed the free text in the occurrence record *locality* data field (550,999). Records located outside the boundaries of the Australian mainland or Tasmanian landmasses were also removed (469,574) using the *over* function from the *sp* R package (Pebesma et al. 2012). Finally, species with less than six mainland observations were removed (matching the minimum adopted for island species), leaving 1530 species and 469,511 occurrences.

2.5 | Testing Endemics

This analysis has used occurrence data on the Australian mainland and coastal islands. But it is possible that temperature ranges may be wider for species when incorporating occurrences outside Australia. Therefore, we repeated the analysis on a subset of 225 species in our dataset identified as endemic by the endemic species list for Australia from the GIFT database (Weigelt et al. 2020) accessed through the GIFT R package (Denelle et al. 2023). The results, summarised in Table S2, show no apparent differences to the full analysis.

2.6 | Rarefied Sampling and Comparison Statistics

The number of mainland occurrences per species (mean of 257, median of 193) was generally much larger than the number of island occurrences (mean of 27, median of 12) in our dataset. This would be expected to produce wider estimated temperature ranges for mainland species by chance alone (See Results Table 1). To make a fairer comparison, we used rarefied sampling. Random samples of mainland occurrences were taken using the number of island occurrences for each species. This was repeated 1000 times, and species means for each variable (MAT, MTWM, MTCM and ΔMAT) were calculated.

2.7 | Distance to the Nearest Mainland Occurrence

Distances in meters from each island to the nearest mainland occurrence for each of the 1530 species were determined using the *st_distance* function from the sp package, using the coordinates of the centroid of the island and the cleaned mainland occurrence records for each species described above.

2.8 | Logistic Regression Models

The factors controlling island colonisation were explored using logistic regression of species presence and absences on islands. From the source pool of the 1530 island species in this study, we tested the effect of distance to the nearest mainland location of species occurrences in a logistic model. We also tested models for distance plus various other predictor variables: the difference in MAT of the island to the mean MAT of all mainland species occurrences, the seed dry mass of species and the maximum potential height of species. These models were repeated for subgroups of the species list—fleshy fruited species only, woody or herbaceous species only

TABLE 1 | The mean difference in temperature range statistics between mainland and island populations for 1530 species distributed across 843 of Australia's islands.

	Mean difference (°C)	Mean difference rarified sampling (°C)	Standard effect size rarified sampling (°C)
Δ MAT	−5.94 (3.45)***	−2.36 (2.25)***	−2.13
Minimum temp coldest month	8.75 (3.61)***	6.36 (2.99)***	6.27
Minimum MAT	4.34 (2.79)***	2.17 (1.95)***	2.37
Maximum MAT	−1.6 (1.82)***	−0.2 (1.57) (n.s.)	−0.86
Maximum temp warmest month	−6.66 (3.17)***	−4.63 (2.98)***	−5.46

Note: MAT stands for mean annual temperature and ΔMAT represents the difference between minimum and maximum MAT. Positive mean differences imply higher *island* temperature statistics, while negative differences imply higher *mainland* temperature statistics. Numbers in parentheses are the standard deviation; n.s. is not significant ($p > 0.05$).

***Represents highly significant differences in a two-sample *t*-test ($p < 0.001$).

and also species only occurring on the east coast of Australia. This final grouping was largely to test the influence of temperature on island occupancy for a geographic coastline running north–south along a latitudinal gradient. The trait variables to predict island occupancy were selected because of their association with island occupancy in island systems (Schrader et al. 2023a).

To fit the models, a matrix of the $\log_{10}$ transformed distance to the nearest mainland occurrence of each species to each island in the dataset was constructed, with a qualifier identifying whether the species was present on the island or not. A logistic regression model was then fitted to the log-odds of a species being present on an island along a continuous gradient of distance to the nearest mainland occurrence plus various temperature and trait variables described above. Examples of this technique can be found in Appendix S1 of (Schrader et al. 2019). Pseudo-R^2 statistics for each logistic model represent the difference in variation explained in comparison to the null model (an even chance of occurrence).

$$\text{Pseudo} - R^2 = \frac{(\text{Null deviance} - \text{Residual deviance})}{\text{Null deviance}}$$

Statistics and plots were completed using R v. 4.4.0 with the stats calculated using *t.test* and *sd* functions in base R, binomial models using the *glm* function and the 95% CI of covariates using the *emmeans* function from the *emmeans* package (Lenth et al. 2024).

3 | Results

3.1 | Island Distributions Extend Less Far Into Cool Temperatures Than on the Mainland

The temperature range of species on islands was generally narrower than their observed range on the mainland. The difference arose from contraction at the cool end of the temperature range (Column 1 in Table 1). This was not only because of a smaller sample size for island versus mainland occurrence datasets. When mainland occurrences were subsampled to the same number as for islands (rarefaction, Column 2 in Table 1), mainland minimum MAT still averaged 2.2°C cooler than islands. The narrower range was evident in both woody and herbaceous species and regardless of the location or climate (Figure 2), although the magnitude of the difference was on average less in woody species (Welch t-stat: 4.3, df: 1629.7, $p < 0.001$). In contrast, there was no difference observed at the warm edges of species under rarefaction (Column 2 in Table 1). This phenomenon was consistent across other temperature metrics such as minimum temperature of the coldest month (MTCM) and maximum temperature of the warmest month, with MTCM and MTWM more extreme (wider apart) for species at mainland sites than on islands.

If temperature boundaries were determined by MTCM, then the cool edge of distributions ought to extend to lower MAT on islands than on the mainland, because MTCM is closer to MAT on islands. However, the opposite was observed. The difference between island and mainland temperature ranges at the cool edge was considerably stronger for MTCM than for MAT (Table 1).

3.2 | Distance to Mainland Populations Predicts Island Occupation Across all Plant Species

Distance to nearest mainland population was a strong predictor of island occurrence (probability of ca 0.5 at 1 km, declining to ca 0.2 at 10 km. Pseudo-R^2 of 0.21; Figure 3). Closer proximity of islands to mainland populations implies similarity of environmental variables such as temperature as well as greater probability of colonisation due to dispersal to the islands. Consequently, we tested logistic models that also included the temperature difference between island and mainland populations, traits such as seed mass or grouping species by growth form or geographic locations (Table S4). However, geographic distance to mainland populations proved to be the most parsimonious predictor over all species in our dataset.

3.3 | Islands at the Cooler End of Species Temperature Range Are no Further Away From Mainland Populations

Given the importance of distance in predicting island occupation, an alternative hypothesis for the shrunken cool edge distributions might be that cool edge islands lie further away from mainland populations in Australia. We compared distances from mainland populations to islands towards the cool end of

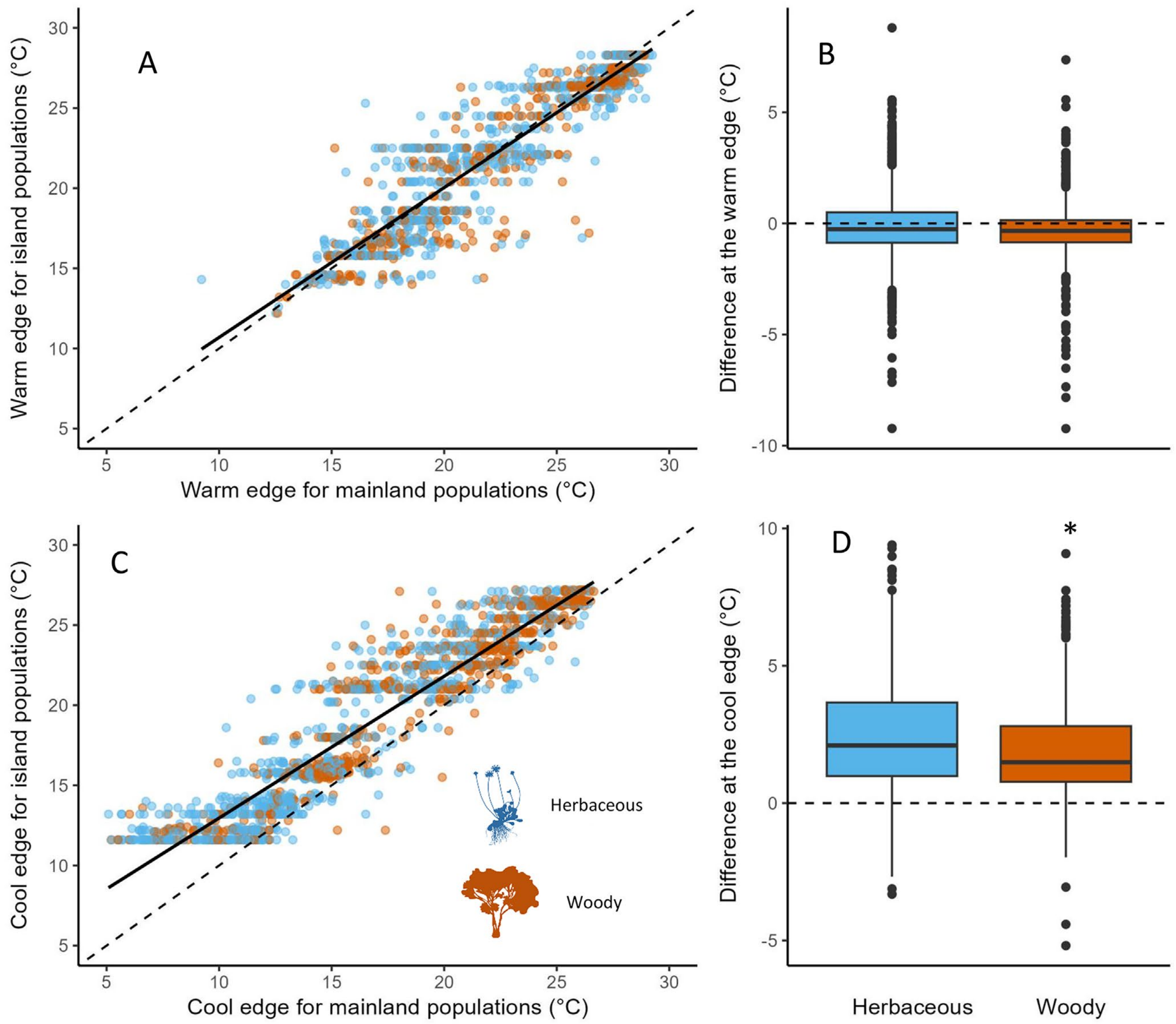

FIGURE 2 | Correlation of island versus mainland temperature ranges for 1530 island species from across Australia. Colours represent (blue) herbaceous and (orange) woody species. Dotted lines indicate a 1:1 correlation line, while solid lines represent a linear model of the pooled woody and herbaceous species. (A) The highest MAT of species on islands compared to the highest MAT of the same species on the mainland and (B) the difference between highest MAT of island and mainland populations for herbaceous and woody species. (C) the difference between lowest MAT of island and mainland populations for herbaceous and woody species. (D) The lowest MAT of species on islands compared to the lowest MAT of the same species on the mainland. Significant difference in D ($p < 0.001$) is represented by *. Horizontal lines of points are due to some islands representing the temperature range limits of many plant species.

the species range (Figure 4A–C) with distances within their temperature range. Cool-range islands were not statistically more remote (Figure 4D; on average 49 ($10^{1.69}$) vs. 48 ($10^{1.6}$) km respectively).

3.4 | Dispersal Mechanisms Did Not Correlate With Temperature Niche Fill

Species were incident on islands towards the cold edge to a varying degree (Figure 2C). Might dispersal mechanisms have been responsible for the variation in niche fill, or in this case, the gap at the cool edge? No correlation was found between the extent of occupying cooler end islands and dispersal syndrome or fruit fleshiness (Figure 5A,B), with no single dispersal mechanism resulting in significantly more complete niche fill than others. Species adapted for dispersal by ants were associated with islands closer to mainland populations (myrmecochory significantly different from all other groups), but otherwise no syndrome seemed notably more effective for dispersal to islands further away from mainland populations (Figure 5C).

4 | Discussion

This study looked for evidence of temperature range expansion or contraction for species across many islands at the continental

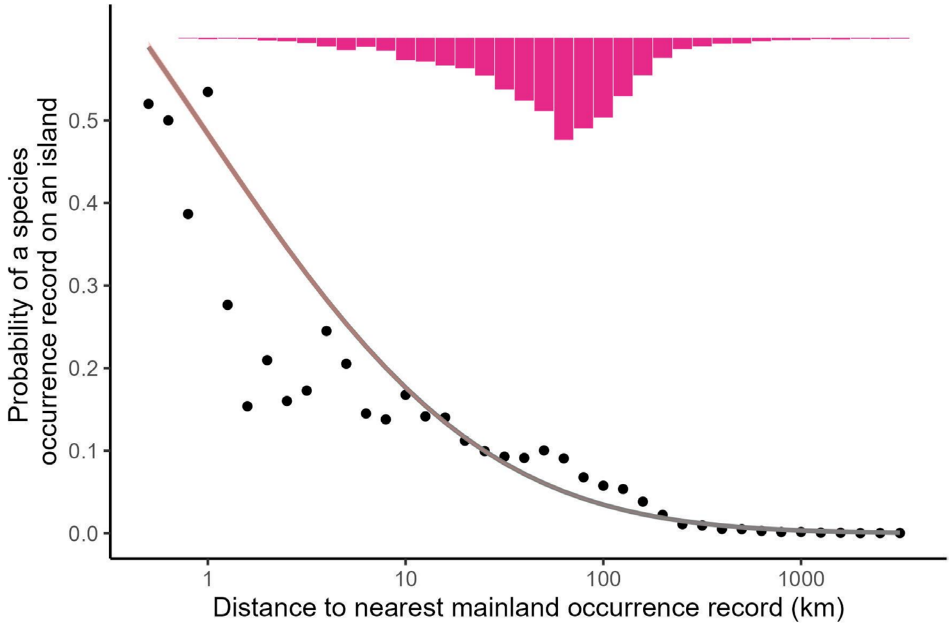

FIGURE 3 | Binomial logistic regression models of island occurrences (grey line) explained by the distance to the nearest mainland occurrence for all species on all islands. Pink bars represent the relative density of island occurrences and shading close to the model represents the 95% CI for the model. Points represent the odds of occurrences versus absences. Pseudo $R^2 = 0.21$.

scale and found species demonstrate a contracted cool edge (conceptual diagram Figure 1, blue symbols) and no evidence for expansion at the warm edge. This finding provides no evidence that species may be able to tolerate warmer temperatures under future climate warming scenarios, but rather that colonising new habitat patches towards the cool edge of species ranges—the leading edge for climate change migration—may be challenging. The underlying reasons for why this phenomenon exists only at the cool edge are not yet clear. Distance to mainland populations was important in predicting island occupancy but was not responsible for the contracted cool edge, which could be due to lower colonisation or higher extinction rates or both.

Our data suggest that species experience no benefits from ecological release on islands and that the theory of ecological release is unlikely to generalise across large numbers of species on continental islands. For this set of Australian plant species, the processes limiting warm-edge ranges were similar on both islands and mainland (Figure 2A) (García-Verdugo et al. 2017; Meredith et al. 2019). The ecological release hypothesis is that if competitors or enemies do not establish on an island (Whittaker et al. 2023) then focal species can extend their range into environments that on the mainland would be occupied by more competitive plant species or by range-restricting enemies. Most studies arguing for diminished competition giving rise to an expanded fundamental niche on islands focus on small subsets of invasive species on oceanic islands isolated from continents by hundreds to thousands of kilometre (Barton and Wong 2019; Caujapé-Castells et al. 2010). However, continental islands differ from oceanic islands in that they experience frequent migration and extinction of species (Morrison 2017; Panitsa et al. 2008; Schrader et al. 2023b). Perhaps ecological release is only possible in communities that are sufficiently isolated and therefore sufficiently different from the mainland, such as might be found on oceanic islands. Furthermore, it might only be applicable to a certain subset of species in certain situations, rather than all plant species and lifeforms as assessed in this study. Such a finding would suggest that for plant communities in small patches of habitat on the mainland, there is no evidence that they will tolerate warmer conditions under future climates.

In contrast, the fact species tend not to inhabit islands towards the cool edge suggests that tracking their climate niche poleward across landscapes of fragmented habitat may be challenging for plant species as they experience climate warming. More than 90% (1412 of 1530) of species in this study demonstrated a contracted cool edge of their range on islands compared to the mainland in comparison to ~60% at the warm edge, with an expected null hypothesis of 50% (Figure 2A,B—if there were no difference, points would regress along the dotted 1:1 line of mainland and island temperature range limits).

This gap at the cool edge averaged at 2.2°C, equivalent to a cool edge of roughly 5° of latitude or about 4–500 km nearer the equator. Investigations into the likelihood of plant species keeping up with climate warming have identified well-dispersed generalists with good colonising ability as having the greatest chance of being able to overcome the barriers to dispersal and colonisation of new habitats (Corlett and Westcott 2013; Neilson et al. 2005). This may include many species in this study that have demonstrated strong colonising ability, as we know they occupy at least six islands. The fact that these species still tend not to extend as far south as on the mainland where in the past (pre colonisation of Australia) there would have been more contiguous habitat, suggests that the ability to overcome the filter of insularity does not necessarily mean better temperature niche fill of isolated habitats. The more fragmented post-colonial habitat of natural vegetation patches in Australia may cause a slower rate of

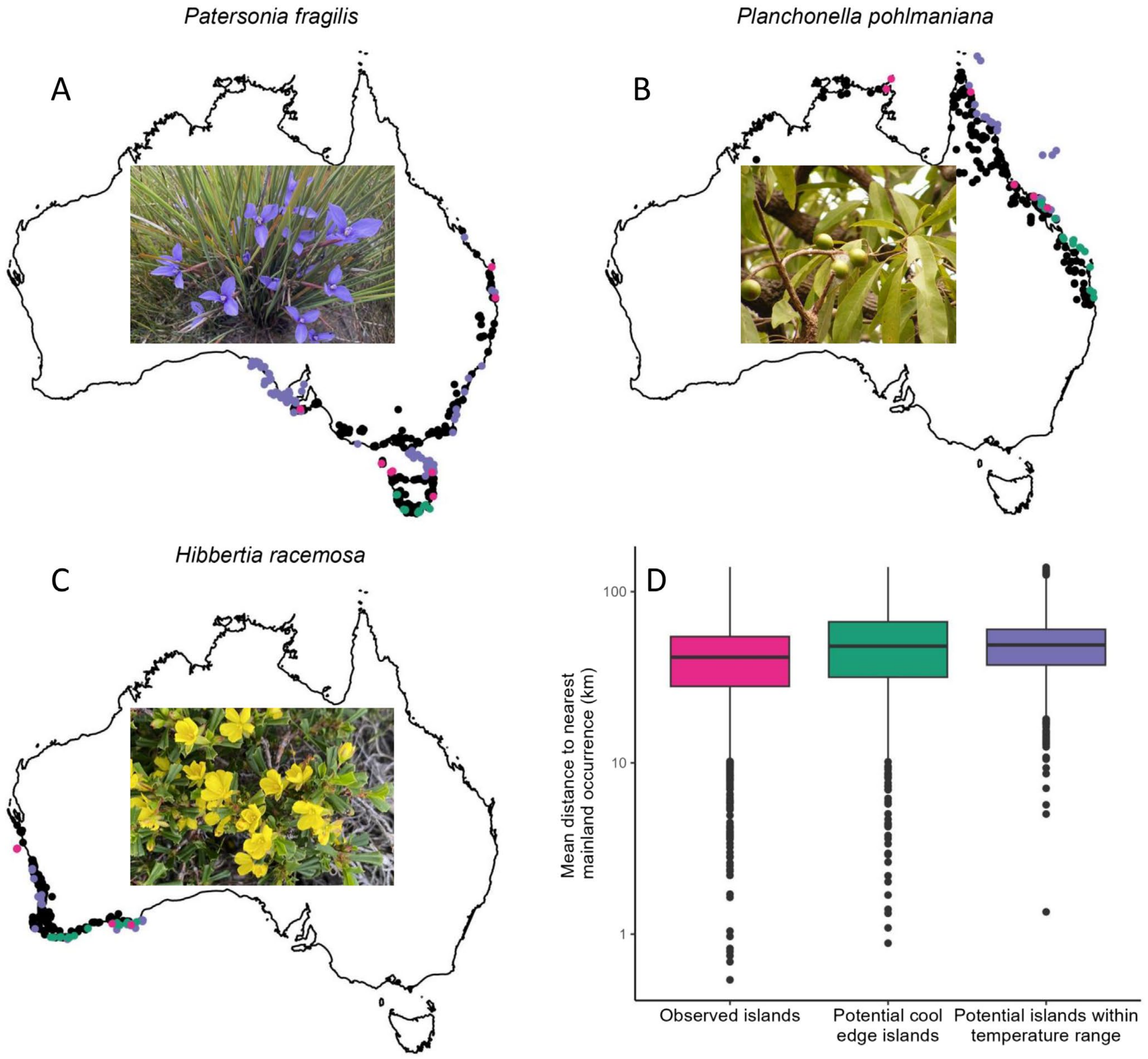

FIGURE 4 | (A–C) Islands within the mainland temperature range of example species *Patersonia fragilis, Planchonella pohlmaniana* and *Hibbertia racemosa*, divided into three groups: islands where the species has been observed (pink), islands with mean annual temperature within the island temperature range (purple) and islands with MAT below the island temperature range but within the mainland temperature range (green). (D) The mean distance from the nearest mainland occurrence to the groups described above. Photos sourced from iNaturalist: *P. fragilis* Gina Hopkins, *P. pohlmaniana* coenobita, *H. racemosa* Bushman.

migration for species than expected at the leading (cool) edge with future climate warming.

The underlying cause of the gap at the cool edge for plant species is not clear. The variety of forms and traits of these plant species and locations that demonstrated this pattern is remarkable—from trees to small herbs and from species occupying islands in tropical to cool temperate climates (Figure 4A–C). Such variability in species points to some geographic factor common to islands rather than biological traits of species. Indeed, we found the most important factor underpinning geographic range on islands was distance from a species' mainland population (Figure 3). However, despite the strong relationship between distance and occupancy, islands at the cool edge did not appear to lie further away from mainland populations than in other parts of the range (Figure 4D).

Perhaps dispersal could help explain the gap at the cool edge. Dispersal traits as factors to explain island occupancy have been assessed at the plant family level globally and at the species level within single archipelagos (König et al. 2021; Leo et al. 2021). Our findings agree with these studies that no single dispersal syndrome is advantageous for niche fill on islands, although ant-dispersed seeds occupied islands situated closer to mainland populations than other syndromes (Figure 5C). Similarly, seed mass, a related dispersal trait, contributed only marginally (weakly to insignificantly) in predicting island occupation (Table S4). There are two factors that may be relevant to

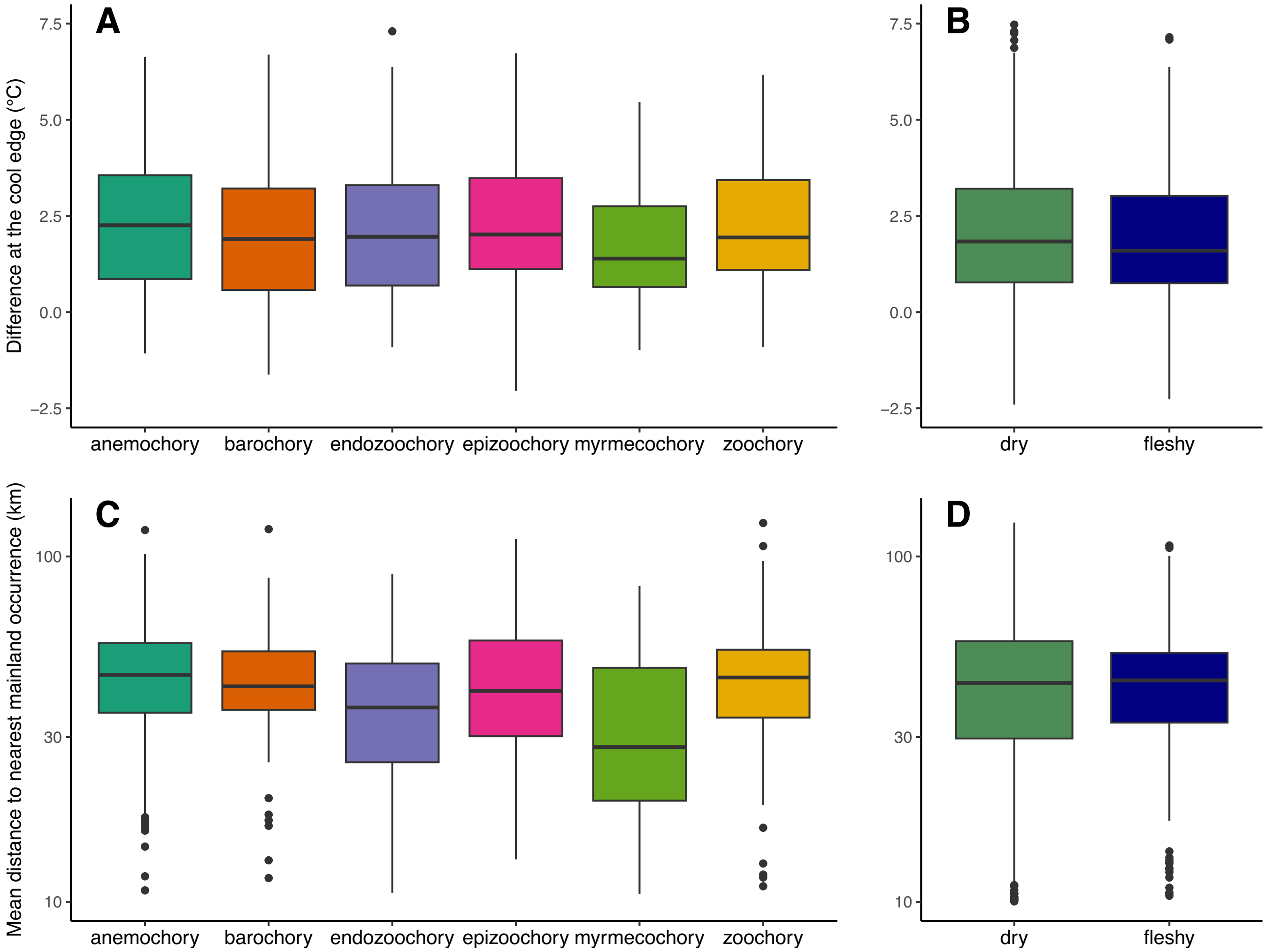

FIGURE 5 | Species differences in minimum MAT between their island and mainland populations grouped by (A) dispersal mechanism and (B) fruit fleshiness and the mean distance to nearest mainland occurrence from their island occurrences grouped by (C) dispersal syndrome and (D) fruit fleshiness. Significant difference in C is represented by *. The *n* species of groupings are anemochory: 182, barochory: 66, endozoochory: 148, epizoochory: 83, myrmecochory: 45 and zoochory: 77; dry: 1316 and fleshy: 276.

explaining why the mean differences in dispersal traits and fruit fleshiness are so consistent in terms of dispersal distance and niche fill. Firstly, the subset of species here are those that have demonstrated they are able to colonise islands and are able to do so regardless of life form, dispersal syndrome or seed traits, etc.; we are comparing species with very similar colonisation abilities regardless of traits. Secondly, we are comparing island occupation on hundreds of islands over very different archipelagos that may have different selection criteria. For example, in some locations, bird dispersal may be most important, while in others, wind may be the dominant vector for seed arrival. Therefore, the mechanisms through which plants arrive might relate less to the dispersal syndrome classification and more so to stochasticity unrelated to seed anatomy (König et al. 2021).

If the majority of species present on these islands reached them during the last glacial maximum 20,000 years ago and remained there, this is a possible explanation for the gap at the cool edge. If this scenario were true, species may have been able to migrate further south as the climate warmed on the mainland, but species trapped on islands could not. However, from repeat surveys of these and other island systems it has been demonstrated that these small coastal islands (more than 95% are less than 2 km^2) have a high rate of turnover, repeated extinction and colonisation over decadal timescales (Flood and Heatwole 1986; Morrison 2017; Panitsa et al. 2008); we observed a mean of 50% turnover of species on islands over 30 years for the islands in the A-Islands dataset. Even when only species that showed evidence of colonisation or extinction over the last 80 years were analysed separately, cool edge islands are still underrepresented (Table S3). Other reasons for species not to inhabit cool edge islands can be grouped by either higher extinction rates or lower colonisation rates. Faster extinction rates could occur if species are present on islands at lower abundances towards their cool edge, making them more vulnerable to extinction-inducing weather events (Wood et al. 2017). Slower colonisation might result from reduced seed output from mainland source pools at cool edges in comparison to the rest of species ranges. There is some evidence that plants closer to the equator commit more energy into seed production (Moles et al. 2009) and it is possible that the latitudinal gradient in seed production may vary within each species as well as in total seed production of plants. These theories are largely speculative and explaining the mechanism behind the gap at the cool edge will require further investigation, including variation in population abundance and reproductive output across species island ranges.

5 | Conclusion

This large continental scale study on the temperature ranges of species across islands has shown that the theory of ecological release is not a dominant process for coastal island plant species. In contrast, species demonstrated a contracted range at the cool edge of species ranges. The gap at the cool edge could have important consequences in fragmented landscapes on the mainland, as well as on islands. This is the leading edge for migration of species as they track their climate niches polewards under climate warming scenarios (Corlett and Westcott 2013; Neilson et al. 2005). Our results suggest that poleward migration between habitat patches may be challenging for plants and require close proximity to larger populations to persist in new habitat fragments. This comes with the implication that active and ongoing management might be helpful to disperse and maintain remote populations for conservation efforts towards the cool edge of species ranges.

Author Contributions

All authors conceived the idea of this study. J.S. and D.C. assembled and processed the data. D.C. analysed the data and wrote the first draft of the manuscript, and J.S. and M.W. contributed substantially to interpretation, concepts and revisions.

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Data Availability Statement

The data and code used in this analysis are available in the Figshare repository found at https://doi.org/10.6084/m9.figshare.28427060.v2 The A-Islands database is a separate body of work published in the Journal of Vegetation Science https://doi.org/10.1101/2024.08.29.609992 and on Zenodo: https://zenodo.org/records/10775810.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.