Title: Are Australia's volcanic-forests "biogeographic continental islands"?

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Data availability

The data that support the findings of this study are available in Dryad at DOI: 10.5061/dryad.kprr4xhdm [currently private for peer review].

These data were derived from the following resources available in the public domain: Wildnet (https://qldspatial.information.qld.gov.au/catalogue/custom/detail.page?fid={40D75ED6-3959-41EB-A5C8-E563FA5B66CA), Natural Values Atlas (https://www.naturalvaluesatlas.tas.gov.au), Victorians Biodiversity Atlas (https://www.environment.vic.gov.au/biodiversity/victorian-biodiversity-atlas), Bionet Atlas (https://www.environment.nsw.gov.au/topics/animals-and-plants/biodiversity/nsw-bionet/about-bionet-atlas), and Australian Virtual Herbarium (https://avh.chah.org.au/).

Abstract

This study investigates whether Cenozoic volcanic complexes in eastern Australia act as biogeographic islands, fostering high levels of terrestrial vascular plant endemism and range-restricted species compared to surrounding sedimentary landscapes. Over six million herbarium records were analysed to assess range-restriction using area of occupancy (AOO) and extent of occurrence (EOO). Georeferenced weighted endemism (GWE) identified centres of endemism, while random forest models explored the environmental drivers of range-restriction, incorporating climatic, topographic, and soil variables.

Results indicate that species on volcanic lithologies were more range-restricted, with smaller AOO and EOO, compared to those on sedimentary units. Seventeen of the 31 volcanic complexes analysed exhibited greater species insularity than their surrounding landscapes. Volcanic complexes such as Atherton, Tweed, Glass House Mountains, and Tasmania were identified as key centres of endemism. Random forest models revealed that climatic and topographic factors, such as precipitation and terrain ruggedness, were stronger predictors of species distributions than volcanic lithology alone.

The findings suggest that volcanic complexes in eastern Australia exhibit varying degrees of insularity, driven primarily by environmental conditions rather than the volcanic substrate itself. These volcanic ecosystems play critical roles in supporting Australia's biodiversity, with broader implications for biodiversity conservation in isolated ecosystems globally.

Keywords: endemic, endemism, centres of endemism, species distribution, range-restricted, vascular plants, biodiversity, volcanic, lithology, volcanic-forest

1 Introduction

The Cenozoic (66 million years - present) volcanic landscapes of eastern Australia are ecologically very different from the largely sedimentary matrix they are embedded in. These Cenozoic volcanic lithologies, spanning the entire length of eastern Australia (Figure 1), formed partly during Australia's separation from Gondwana as it migrated over a volcanic hotspot (Davies et al., 2015; Wellman & McDougall, 1974). The forests on these landscapes, hereafter referred to as "volcanic-forests" include eucalypt forests, and some rainforest and natural grasslands that are underlain by igneous extrusive volcanic parent material. The volcanic-forests are areas of high species richness and often contain high phylogenetic diversity, exemplified by the Wet Tropics and Gondwana Rainforests of Australia (Kooyman et al., 2013; Thornhill et al., 2016).

This combination of taxonomic and phylogenetic diversity creates regions that are also centres of endemism, potentially due to high speciation rates and biogeographic, biotic, or abiotic factors that limit species distribution (Qian et al., 2023). Endemic species typically have small geographic ranges and narrow habitat specificity, making them highly adapted to specific environmental conditions and vulnerable to changes (Rabinowitz, 1981). Climate change disproportionately affects endemic species, particularly those in mountaintop regions (Costion et al., 2015a; Laidlaw et al., 2011; Williams et al., 2003). Therefore, assessing endemism is crucial for conservation as it represents unique biodiversity, especially in Australia where many species are endemic and under-assessed for threats (Gallagher et al., 2023).

Following the foundational work of MacArthur & Wilson (1967) , who noted that island biogeography theories could be extended to any kind of isolated habitat, Kruckerberg (1991) introduced the idea that geoedaphic factors, such as volcanic lithologies, can create "mainland islands" where isolated pockets of unique environmental conditions drive speciation and endemism. Kruckeberg & Rabinowitz (1985) demonstrated that such isolated landscapes foster high biodiversity by supporting narrow endemic species in specialised ecological conditions, a concept further explored in island-like systems, as reviewed by Itescu, (2019). We suggest that volcanic-forests may function as mainland islands because the contrast between volcanic geologies and surrounding sedimentary geologies may limit species migration, leading to high levels of biodiversity and endemism.

While lithology's role in shaping endemic flora has been documented (Kruckerberg, 2002; Sutherland, 2011), the specific influence of Cenozoic volcanic lithologies in eastern Australia remains less understood. Eastern Australia has seven recognised endemic centres (Crisp et al., 2001), five of which are on Cenozoic volcanic complexes: the Wet Tropics, Border Ranges (McPherson-Macleay), New England-Dorrigo, Australian Alps, and Tasmania. Furthermore, the 'Forests of East Australia', which encompasses the first three centres identified, is recognised as a global biodiversity hotspot, with at least 1500 endemic species (CEPF, 2024; Williams et al., 2011). Lithology's influence on endemic flora in eastern Australia has been documented in specific systems such as granite inselbergs (Hunter, 2016), serpentine (Batianoff et al., 1997; Specht et al., 2001), and dolerite (Kirkpatrick & Brown, 1984). In eastern New South Wales (NSW), vegetation distribution closely aligns with lithology type (Keith, 2011), with high floral turner linked to lithology and elevation (Di Virgilio et al., 2012). However, these studies have primarily examined specific lithologies, often overlooking the broader geological phenomenon of Cenozoic volcanic complexes.

Australia's volcanic-forests, spanning more than 3,000 km, are part of a larger geological narrative involving multiple volcanic hotspot tracks (Figure 1; Davies et al., 2015). Over time, these volcanic complexes, often forming mountainous areas, have eroded to produce fertile soils. Due to their relative isolation and geological history, these volcanic complexes may serve as refuges for endemic species (Crisp et al., 2001; Weber et al., 2014), particularly those with narrow ecological niches, functioning similar to islands within a matrix of diverse landscapes. Although the east coast's mountainous areas are not particularly elevated by global standards, even low-lying mountainous areas such as those formed by extensive basalt plains in eastern Australia, have the potential to act as refugia as shown in southwestern Australia (Keppel et al., 2017). However, research into the potential of these elevated regions as refugia have primarily focused on the Tweed volcanic complex (Weber et al., 2014) and Atherton (Costion et al., 2015b), leaving other volcanic complexes largely unexplored.

This study investigates whether volcanic complexes in eastern Australia act as biogeographic islands with varying degrees of insularity, influencing endemicity patterns through environmental factors. We hypothesise that the volcanic-forests harbour more range-restricted species than the surrounding vegetation. Volcanic complexes that function as refugia are expected to have all species, including exclusive species, showing smaller Area of Occupancy (AOO) and Extent of Occurrence (EOO) on the outcrop compared to the surrounding landscape matrix. Furthermore, we aim to understand the relative importance of these unique ecosystems and their influence on patterns of endemicity in eastern Australia for better conservation management. By focusing on a fine-scale resolution of 10 km, instead of the larger grid cells (e.g., ~110 km) used previously in foundational studies such as Crisp et al. (2001), we aim to capture detailed patterns of endemism, including local patterns and fine grain comparison with environmental variation. Utilising updated herbarium data (over 6 million data points) and metrics such as Geographic Weighted Endemism (GWE), which considers species' extent of occurrences, this research provides a deeper understanding of Australia's biogeographic islands and drivers of endemicity. Formally, our research questions are: 1) Do Cenozoic volcanic complexes harbour a higher number of range-restricted species than the surrounding landscape? and 2) How do the levels of endemicity in volcanic-forests compare to those in the broader flora of eastern Australia?

2 Methodology

2.1 Study Area and Scope

This study focuses on the eastern Australian states of Queensland, New South Wales (including the Australian Capital Territory), Victoria, and Tasmania where approximately 98% of the Cenozoic volcanic surface lithologies on the continent have been identified using Geoscience Australia's Surface Geology dataset (Raymond et al., 2012). The Cenozoic volcanic lithologies have historically been classified into three categories: Basalt Lava Fields, which are extensive mafic lava fields; Central Volcanoes, which are bimodal volcanoes with both mafic and felsic lavas; and the Leucitite Suite, which are mafic deposits characterised by high concentrations of leucite (Wellman & McDougall, 1974). We specifically examine the floras associated with these Cenozoic volcanic formations, including the bimodal Central Volcanoes and mafic Basalt Lava Fields. The Leucitite Suite is excluded from our insularity analysis because little of this geology retains native vegetation.

Mafic rocks, particularly basalt, are richer in essential nutrients (magnesium, calcium, phosphorus), enhancing soil fertility. In contrast, felsic rocks (e.g., rhyolite) have higher potassium but lower levels of other essential nutrients, leading to less fertile soils (Gray et al., 2016). Thus, it is essential to compare different types of volcanic floras with the surrounding non-volcanic flora to understand the ecological and biogeographical significance of these volcanic features in the broader landscape.

2.2 Data Collection and Cleaning

Occurrence (presence-only) data of all vascular plant species were collated from state-based herbaria and databases of field surveys across eastern Australian to ensure a wide coverage of endemic species distributions. Data sources included Queensland WildNet (Department of Environment and Science, Queensland Government, 2022), NSW Bionet Atlas (including ACT observations) (Office of Environment and Heritage, 2024), Victorian Biodiversity Atlas (Department of Energy, Environment and Climate Action, 2024), Tasmanian Natural Values Atlas (Department of Natural Resources and Environment Tasmania, 2024), and the Australasian Virtual Herbarium (AVH) (Council of Heads of Australasian Herbaria, 2022a). Taxonomic verification used the Australian Plant Census (Council of Heads of Australasian Herbaria, 2022b), and non-native species were removed using multiple databases (Martín-Forés et al., 2023; Randall et al., 2023; Slatyer, 2024). Weeds from the Weeds of National Significance list (Invasive Plants and Animals Committee, 2016) and other state-specific lists were also excluded (Department of Natural Resources and Environment Tasmania, 2024; Business Queensland, 2024a, 2024b; Department of Primary Industries, New South Wales, 2024; Agriculture Victoria, 2024). Bryophytes and fungi were filtered out using the Australian Bryophyte Census and Fungi List (Council of Heads of Australasian Herbaria, 2024). Observations were filtered to the species level, removing genus-only and infraspecific taxa. To focus on intact vegetation, observations from non-natural areas (e.g., cropland, built-up areas, aquatic environments) were excluded using ESA WorldCover data at a 10-metre resolution (Zanaga et al., 2022).

In regions with insufficient sampling, AOO and EOO may underestimate species distributions, leading to false gaps in the data due to detection errors or lack of survey effort. This is especially problematic for rare or less-studied species, which often have incomplete data. To address this, we excluded species with fewer than ten occurrence records to ensure that AOO and EOO accurately reflected species distributions and to avoid skewed results from small sample sizes. In total, 997 species were removed. Many of these were species that occurred at state borders, including 591 shared between the Northern Territory and Queensland, and 221 shared between South Australia and Victoria, where data was limited. Although this conservative filtering step inevitably excluded some genuinely rare species, it helped mitigate the larger impact of incomplete sampling. After this adjustment, 11,136 species were retained for further analysis.

2.3 Assessing Spatial Autocorrelation

Understanding spatial autocorrelation is crucial for validating observed patterns, ensuring they are driven by spatial processes rather than random distribution or uneven sampling. We accounted for spatial autocorrelation by calculating Moran's I. This metric ranges from -1 (perfect dispersion) to 1 (perfect clustering), with 0 indicating a random pattern (Legendre & Fortin, 1989). By calculating this, we can adjust for potential biases, ensuring accurate interpretation of spatial trends.

2.4 Measures of Endemicity

Endemism is a scale-dependent concept (Hobohm & Tucker, 2014a). Thus, areas of high endemism can vary significantly depending on the spatial scale of analysis, from small volcanic complexes to large biogeographic regions (Daru et al., 2020). Additionally, the percentage of endemic species in any specified area depends on its location, the group of organisms considered, and its position in geological time; that is, species can be endemic to a certain habitat rather than geographic area (Anderson, 1994). Measuring endemicity involves various methods and indices to accurately reflect the extent and concentration of species within defined boundaries (Hobohm & Tucker, 2014b; Shipley & McGuire, 2022). Importantly, endemism concepts have been extended numerically to provide continuous metrics based on species range restriction, rather than categorical counts of *a priori* determined endemic species (Guerin & Lowe, 2015). To answer our research questions, we examined both ecological and geographic concepts of endemism; endemicity to volcanic lithology as a form of ecological endemism, and endemicity to individual volcanic complexes and bioregions as geographic endemism. This approach allowed us to identify persistent areas of endemism across various scales and factors.

2.4.1 Exclusivity to Lithology

The Surface Geology of Australia 1:1 million 2012 dataset (Raymond et al., 2012) was intersected with all terrestrial vascular plant occurrence records, and the Lithology attribute was reclassified into four categories: igneous, metamorphic, sedimentary, and other. The igneous category was further subdivided into volcanic (mafic, intermediate, felsic), intrusive (mafic, intermediate, felsic), bimodal (containing both mafic and felsic material (Ewart et al., 1985)), and volcanic-sedimentary mix (containing both volcanic and sedimentary units). This subcategorisation of igneous units allows us to compare Cenozoic volcanic complexes (predominantly extrusive) to their intrusive equivalents (such as comparing basalt to gabbro and rhyolite to granite) and mixed units for differences in ecological impact. Species exclusive to a particular lithology were identified as those with 100% of their occurrence on one lithology type. Species with at least 95% of their occurrences on one lithology type were classified as having a predominance for that type.

2.4.2 Insularity

The AOO and EOO values for each species were calculated using the ‘red’ R package (Cardoso & Branco, 2023) based on IUCN definitions. Determined at a 2×2 km grid resolution, AOO represents the total number of grid cells occupied by a taxon (Cardoso, 2017). This scale ensures consistency and comparability with other studies (IUCN SSC Red List Technical Working Group, 2024). The EOO was calculated as the area of the minimum convex polygon covering all recorded occurrences of the species. Typically, EOO exceeds AOO, but some range-restricted species may have a smaller EOO (<4 km²) due to distribution across multiple grid cells. All species occurring on volcanic complexes and within a buffer zone (calculated as 10% of the longest horizontal distance of the polygon, often resulting in a slightly larger matrix area depending on the shape of the outcrop) were extracted. This allowed for a comparison of the median AOO and EOO of species within the complex to those in the surrounding flora.

2.4.3 Extent and range-restrictedness

Georeferenced weighted endemism (GWE; Guerin et al., 2015) was chosen over other range-size metrics such as corrected cell weighted endemism (CWE; (Crisp et al., 2001)) due to its precise measurement of species' geographic ranges. Unlike CWE, which counts the number of cells a species occupies (reflecting AOO), GWE uses georeferenced data to accurately capture the spatial extent of species distributions. This provides a more robust indication of centres of endemism, defined as areas with a high concentration of range-restricted species, and ensures a more accurate representation of species with restricted ranges; this is crucial for identifying true areas of endemism. GWE for a grid cell i is calculated as:

$$GWE_i = \sum_{j=1}^{s_i} \frac{1}{EOO_j}$$

where S_i is the total number of species present in the grid cell i, j is the index for the species in that grid cell, and EOO_j is the extent of occurrence of species j. GWE was calculated using the weighted.endemism() function in the ‘biomapME’ R package (Guerin, 2022).

Whilst GWE effectively handles incomplete datasets and provide valuable insights into spatial biodiversity patterns (Shipley & McGuire, 2022; Volis & Tojibaev, 2023), weighted endemism scores are influenced by species richness (Crisp et al., 2001; Kier & Barthlott, 2001). A grid with more species has a higher likelihood of scoring higher endemism values simply due to the presence of more species, and this effect is non-linear, as endemic species are more likely to be present in species-rich areas drawn from the regional species pool (Jetz et al., 2004). This inherent bias can obscure true patterns of endemism as distinct from species richness, making it difficult to discern whether high endemism scores are due to high species richness or actual high endemism. Due to its definition, GWE is also sensitive to uneven sampling efforts. We opted not to divide the GWE score by species richness, as proposed by Crisp et al., (2001), for the same reason as Slatyer et al., (2007) who found that CWE significantly magnified the effects of uneven sampling, generating very high endemism scores in poorly sampled areas where widespread species were under-sampled. Instead, permutation tests of the null hypothesis corrected for this bias by generating a null distribution of GWE scores under the assumption of random species distribution (Guerin et al., 2015). By comparing the observed endemism scores against this null distribution, it is possible to determine whether the observed scores are significantly higher or lower than expected given the species richness. The resulting GWE map highlighted grids where there are more species with smaller ranges.

For a species to be considered ‘endemic’, i.e., occurs nowhere else but the defined landscape, it must be range-restricted to something specific (e.g., lithology, volcanic complex or region). Thus, to provide an absolute number of species endemic to an area, we used the Interim Biogeographic Regionalisation for Australia (IBRA version 7) bioregions and sub-bioregions (Department of Climate Change, Energy, the Environment and Water, 2023), and applied a conservative approach to outlier management to maintain a comprehensive representation of species ranges because floral turnover is gradational (Di Virgilio et al., 2012). Specifically, if ≥95% of the species occurrence records fall within the bioregion or sub-bioregion (allowing for occurrences on boundary edges), it is considered endemic. IBRA zones were used because they delineate patterns of biodiversity using lithology/geology, climate, landform, and vegetation community among others (Ebach et al., 2013; Thackway & Cresswell, 1995).

2.5 Predicting range-restrictedness

We used random forest models to predict drivers of range-restriction among species on volcanic complexes, focusing on whether lithology or other environmental factors played a larger role. Random forests were chosen for their ability to handle nonlinear relationships, both categorical and continuous predictors, are generally robust to noise, and can handle large numbers of predictors provided they are not highly correlated (Breiman, 2001). The log-transformed AOO and EOO for 11,136 species were used due to the right-skewed distribution of range sizes.

The environmental variables included topographic, climatic, vegetation, lithology and soil data. Topographic variables included elevation (NASA JPL, 2013), and terrain ruggedness index (TRI) calculated in QGIS (QGIS Development Team, 2023) following the method proposed by Riley et al., (1999). Climatic variables comprised three separate datasets, each with 19 temperature and precipitation-related variables: past climate data from the Last Glacial Maximum) provided by CHELSA using the MIROC-ESM model, which is suitable for Australia (Du et al., 2024), present climate data from 1981-2010 provided by CHELSA (Karger et al., 2023), and the differences between past and present climate data as a proxy for climate stability. Vegetation class (Department of Climate Change, Energy, the Environment and Water, 2020), lithology class (Raymond et al., 2012), and soil class alongside soil physical and chemical properties from the Soil and Landscape Grid of Australia data (Searle, 2021) were included as predictors in the model. A comprehensive list of the variables is provided in the Supplementary Information (Table S1).

To minimise overfitting and ensure model robustness, five-fold cross-validation was used for model selection (Yates et al., 2023), and model evaluation was conducted using RMSE (Root Mean Square Error), MAE (Mean Absolute Error), and R^2 (Coefficient of Determination). RMSE measures the model's prediction error, MAE indicates the average magnitude of errors, and R^2 assesses the proportion of variance explained by the model. Highly correlated variables (Pearson’s $r > 0.7$) were removed prior to cross-validation to improve model performance and reduce multicollinearity. Variable importance was assessed to identify key drivers of range restriction.

3 Results

3.1 Spatial Autocorrelation

The Moran’s I test for EOO (0.146, $p < 2.2e-16$) and AOO (0.124, $p < 2.2e-16$) revealed statistically significant positive spatial clustering. The small degree of clustering aligns with expected patterns for range-restricted species, as their limited spatial extents will naturally result in some clustering. The absence of stronger clustering suggests that the dataset is relatively free from significant sampling bias. This small positive clustering trend is expected and normal, indicating that while some spatial patterns exist, they do not dominate the dataset, thus ensuring its integrity for further analysis.

3.2 Exclusivity to Lithology

We analysed 6,000,146 records (11,136 native species with ≥10 occurrences) from eastern Australia. Thirty-one of these species occur exclusively on volcanic lithologies, showing smaller median AOO and EOO than the 77 species on intrusive and 1,150 species on sedimentary units (Figure 2; Table S2). Volcanic-exclusive species exhibited more restricted distributions, while sedimentary-exclusive species generally had larger AOO and EOO values. Additionally, 46 species predominantly occurred on volcanic lithologies, with smaller median AOO and EOO compared to 2,214 species predominantly on sedimentary units (Figure 2). Volcanic species showed greater variability in EOO but had generally lower values than sedimentary species. Species richness was highest on sedimentary (10,885) and intrusive (8,816) lithologies, both having larger median AOO and EOO values. In contrast, volcanic lithology (8,500 species) had smaller median AOO and EOO, and mixed volcanic-sedimentary lithology (3,983 species) also exhibited smaller median AOO and EOO compared to sedimentary units.

An analysis comparing AOO and EOO between mafic and felsic volcanic species indicated that volcanic lithologies exhibited smaller AOO and EOO than intrusive species (Figure S1). This trend suggests a potential link between volcanic lithology and species' range restriction, but additional data are required to confirm the significance of this pattern. Currently, there is insufficient data to make a reliable comparison between species predominantly found on mafic versus felsic volcanic substrates.

3.3 Insularity

Examining individual volcanic complexes and comparing the species on the outcrops to those in the surrounding matrix flora reveals varied patterns in terms of AOO and EOO for both all species and exclusive species (Table S3). Some complexes exhibited consistent trends across both metrics, while others showed mixed signals (Table 1). In several complexes (i.e., Atherton, Canobolas, Comboyne, Hillsborough, Peak Range), all species, including exclusive species, had AOO and EOO smaller on outcrops than in the matrix.

Volcanic complexes consistently showed higher ruggedness and elevation than the surrounding matrix. The median Terrain Ruggedness Index (TRI) for outcrops was 10.1, compared to 9.43 for the matrix. Complexes with consistently higher TRI statistics (median, range, and standard deviation; Table S4) included Hillsborough, Nebo, Bunya, Main Range, Tweed, Canobolas, Dubbo, Liverpool Range, Nandewar, and Warrumbungle. These complexes also had higher median elevations. Twenty-six of the 31 volcanic complexes analysed had higher median elevations on volcanic outcrops, with an average difference of 131 meters, reinforcing their role as inselbergs, and acting as biogeographic continental islands. Dubbo, Piebald, Newer Volcanics, and Older Volcanics had minimal elevation differences due to low regional elevations. An exception is the Sturgeon complex in central Queensland, where the outcrop's median elevation was 603 meters, and the matrix was 666 meters, suggesting the entire region is elevated.

3.4 Endemicity by Extent and Range-restrictedness

The GWE analysis aligns with observed endemicity patterns at the bioregion level but shows stronger alignment at the sub-bioregion scale, emphasising the importance of scale in endemicity analysis. High GWE scores, indicating regions with many range-restricted species (Figure 3a), coincided with areas of high species richness (Figure 3b). The Atherton and Tweed volcanic complexes have the highest GWE levels (Figure 4a). Additionally, the Glass House Mountains, Ebor, Barrington, Nandewar, Warrumbungle, Older Volcanics, Newer Volcanics, and Tasmania volcanic complexes exhibited higher endemicity scores compared to their surrounding regions (Figure 4), although not as pronounced as those in the Atherton and Tweed complexes. Non-parametric tests confirmed the significance of GWE scores in volcanic-forests, with these areas appearing as upper outliers, exceeding 1.5 times the interquartile range of the null distribution given the species richness for that grid cell (Figure 3d).

Four bioregions stood out for their disproportionately high levels of endemicity: the Wet Tropics (WET; 662 endemic species; Figure 5a), South Eastern Queensland (SEQ; 307 endemic species; Figure 5b), Cape York Peninsula (CYP; 299 endemic species), and the Sydney Basin (SYB; 245 endemic species; Figure 5c; Table S5 and Table S6). At the sub-bioregion level, high endemicity in the WET bioregion was concentrated in the Daintree-Bloomfield area (85 endemic species), which is predominantly composed of sedimentary and intrusive felsic units, and Bellenden Ker-Lamb (17 endemic species) which extends over parts of the Atherton volcanic complex. In SEQ, endemicity was concentrated in the Scenic Rim sub-bioregion (26 endemic species), home to the Tweed and parts of the Main Range volcanic complexes, which are bimodal and contain both mafic and felsic volcanic units. In CYP, the sub-bioregion with the highest number of endemic species contains 29 endemic species, mostly located in the Iron Range and McIlwraith Range

National Parks, which are predominantly intrusive felsic units. In SYB bioregion, endemicity was concentrated in the Wollemi sub-bioregion (27 endemic species), which is primarily sedimentary. Notably, the Southeast sub-bioregion in the Tasmania Southeast bioregion has the second-highest number of endemic species (Table S6), with 40 endemic species (Figure 5d). However, it was not highlighted in the bioregion analysis due to the overwhelming numbers in other bioregions, which were several orders of magnitude higher (Table S5).

3.5 Predictors of Range-restrictedness

The RFM, applied across eastern Australia, explained up to 37% of the variance in AOO and 8% in EOO. The best hyperparameter tuning grid search result indicated models with an mtry of 1 (favouring many 'stumps' or single predictor models) using 5000 trees, revealing limited predictability. This necessitated regional analyses for complexes with high insularity, where species' AOO and EOO were smaller than the surrounding buffer, indicating potential refugia. We focused on five volcanic complexes: Atherton, Peak Range, Canobolas, Comboyne, and Tweed. In northern Queensland, the mafic Atherton and Peak Range complexes showed a stronger influence of soil parameters (Table 2). In Atherton, annual precipitation differences were key for both AOO and EOO, with warmest-quarter precipitation and soil organic carbon influencing EOO, and coldest-quarter precipitation and available phosphorus affecting AOO. Peak Range showed the importance of terrain ruggedness and soil organic carbon for both AOO and EOO, while wettest-quarter precipitation influenced AOO, and mean driest-quarter temperature differences were important for EOO. In New South Wales, the two bimodal complexes of Comboyne and Canobolas were more influenced by past and present climate conditions (Table 2). For both complexes, the maximum temperature of the warmest month during the LGM was a significant predictor for AOO. In Comboyne, driest-quarter temperature differences were significant for both AOO and EOO, while in Canobolas, annual temperature range and driest-quarter precipitation during the LGM were key for AOO, and differences in mean temperature of the wettest quarter limit the EOO (Table 2).

Lastly, we chose to examine Tweed over Hillsborough because the latter had too few occurrence records (116), to model meaningfully. Tweed's RFM results, based on nearly 800,000 occurrence records, show that past and present precipitation, especially in the wettest quarter during the LGM, drive species distribution (Table 2). Additionally, mean diurnal temperature range affects AOO, and wettest-quarter precipitation influences EOO. Overall, the regional analyses underscore the importance of past and present bioclimatic variables along with soil physical and chemical properties, which may indirectly relate to properties of the underlying geological substrates, but lithology remained a less important factor across all models.

4. Discussion

Volcanic Complexes as Biogeographic Continental Islands

Our study confirmed that many Cenozoic volcanic complexes in eastern Australia function as biogeographic continental islands, supporting higher numbers of range-restricted species compared to surrounding sedimentary regions. From the GWE analysis, we identified widely-recognised centres of endemism, including Atherton, Tweed, Snowy Mountains, Southern Highlands, and Tasmania (Crisp et al., 2001), while also revealing new centres in less-studied volcanic complexes, such as the Glass House Mountains, Main Range, Ebor, Nandewar, Warrumbungle, and Barrington. These results provide a more comprehensive view of the role of Australia’s eastern volcanic landscapes in influencing vascular terrestrial plant species distribution. While we hypothesised that volcanic lithology would play a strong role in shaping insularity, our analysis of species distribution patterns revealed four distinct types of insular complexes that were uncorrelated with lithology types. This indicated that lithology was not the primary driver of plant endemicity patterns in eastern Australia. The RFM confirmed that the drivers of species range (AOO and EOO) vary across complexes, with no single environmental predictor responsible for the observed patterns of endemicity across our study region. Instead, it is a complex interplay of climatic, edaphic and topographic factors, such as elevation and terrain ruggedness, which were more influential in determining the degree of insularity. These findings highlight the need for regionally specific conservation strategies across Australia’s volcanic landscapes, as each complex exhibits unique ecological dynamics.

Our analyses showed that 17 of the 31 volcanic complexes had species found exclusively on volcanic lithology, with smaller AOO and EOO than the surrounding flora. This suggests that many of Australia’s volcanic complexes, through their unique topography and soils, act as continental biogeographic islands, promoting species isolation and endemism. While this aligns with global patterns of insular endemism on unique geological substrates (Kruckerberg, 2002), the extent of these dynamics across such a vast region in Australia suggests a distinct ecological phenomenon. This agrees with other work showing similar confinement patterns in other environments, such as granite inselbergs (Hunter, 2016) and serpentine outcrops (Batianoff et al., 1997). The 31 species that occur exclusively on volcanic lithologies highlight how these environments provide refugial conditions conducive to supporting range-restricted species. Since lithology alone was not the primary driver of insularity, a combination of environmental factors and ecosystem processes are likely at play, such as isolation and long-term climatic stability (Weber et al., 2014).

Four Distinct Types of Insular Complexes

Our insularity analysis categorised volcanic complexes into four distinct types, which reflect the relationship between species' AOO and EOO in the volcanic-forests compared to the surrounding flora. These categories align with Rabinowitz's (1981) forms of rarity, which illustrate the varied ecological roles that these volcanic-forests play. Each type highlights a different aspect of how volcanic complexes function as biogeographic islands.

The first category consists of complexes where both AOO and EOO are larger than in the surrounding matrix. Examples from our study include Chudleigh, Nulla, Piebald, Liverpool Range, and the Newer Volcanics. These complexes host broader and more robust volcanic-forest ecosystems, supporting a wide variety of species, including those exclusive to volcanic outcrops. For instance, Coolah Tops National Park, on the mafic Liverpool Range, supports some of the tallest recorded silvertop stringybark (*Eucalyptus laevopinea*) and snow gum (*Eucalyptus pauciflora*) trees (New South Wales National Parks and Wildlife Service, 2002), within a landscape of open forests and dry rainforests (Benson et al., 2010). These volcanic-forests provide stable habitats for species near the western edge of their moist montane ranges.

The second category consists of complexes where both AOO and EOO are smaller than in the matrix. This group includes Atherton, Hillsborough, Peak Range, Tweed, Comboyne, and Canobolas, which support highly specialised, and potentially more vulnerable, ecosystems. The species within these volcanic-forests tend to be finely adapted to specific environmental conditions. These volcanic complexes act as biogeographic islands, providing crucial refugia through their rugged terrain and higher elevations. Atherton and Tweed, for example, have been recognised as long-term refugia, where stable climates and topographic features have allowed species with highly restricted ranges to persist (Costion et al., 2015a; Weber et al., 2014).

The third category includes complexes where AOO is larger, but EOO is smaller than the surrounding matrix. Bunya, Nandewar, and Nebo are examples of this type. These volcanic complexes support species with limited spatial distributions but larger local populations, suggesting that species in these volcanic-forests may be specialised to thrive under particular local conditions. This pattern indicates that while species may occupy a smaller geographic range, they may be ecologically dominant within their habitat.

The fourth category comprises complexes where AOO is smaller but EOO is larger than the surrounding matrix. Springsure and Tasmania are prime examples, where species may have a narrow occurrence but broader ecological influence. In Tasmania, for instance, paleoendemic species on basaltic outcrops, though not exclusively confined to these areas, persist across a wider range of habitats. The central highlands of Tasmania offer stable climates, persistent moist conditions, and a buffer from fire events, enabling the long-term survival of these paleoendemic species (Jordan et al., 2016). These refugial conditions are expected to continue supporting species under future climate scenarios (Mokany et al., 2017).

Our identification of these four distinct insular types reveals that eastern Australia's volcanic complexes do not operate as uniform ecological entities. Instead, they play diverse roles in supporting endemic species, from broad ecosystems with stable conditions to highly specialised habitats with limited species distributions. This multifactorial nature of insularity likely reflects an interplay of ecological processes, including competition for resources, climate variation, fire dynamics, and land-use changes in driving species distribution. These insights contrast with studies like Hunter's (2017) examination of granite inselbergs in the New England Batholiths, where climatic factors were more directly linked to species persistence. Our larger scale study, spanning the entire east coast of Australia, shows that the volcanic-forests support a range of ecological processes varying in insularity, suggesting that more research is needed to untangle the specific drivers shaping each volcanic complex's species endemicity.

Drivers of Endemicity: It is a Complex Story

The varied drivers of species distribution across volcanic complexes highlight the complexity of these volcanic landscapes. Our RFM indicated that climatic, topographic, and soil factors play a more significant role than geological substrates in shaping species' AOO and EOO. For example, in northern Queensland's Atherton and Peak Range complexes, differences in annual precipitation, especially in the coldest and warmest quarters, were key predictors for both AOO and EOO. Similarly, soil nutrient availability (e.g., phosphorus) was an important factor for species' range sizes, suggesting that local soil fertility interacts with climatic conditions to shape species persistence (Lambers & Oliveira, 2019). Further south, in the bimodal volcanic complexes of Comboyne and Canobolas, historical climate data from the LGM and present conditions were found to be more influential. Past temperature extremes during the warmest and driest months shaped the AOO of species in these areas, while changes in annual temperature range influenced EOO. This suggests that species in these regions are adapted to specific climatic regimes that have persisted over millennia, making them vulnerable to future climate shifts.

In the bimodal Tweed complex, one of the most significant centres of endemism, both past and present precipitation patterns were crucial for determining species ranges. The differences in annual precipitation and the wettest quarters during the LGM were particularly influential for species with restricted ranges. These findings align with previous studies (Das et al., 2019), indicating that climatic stability over long periods has allowed these species to persist. However, the projected impact of climate change, particularly the anticipated reduction of moisture in these already fragile systems, presents a serious threat to the future persistence of these species (Strong et al., 2011).

While climate and topography were important factors in determining species distributions across volcanic complexes, they are not the only drivers, and the full story is more complex. Our results indicate that higher-than-average elevation and terrain ruggedness contribute to microclimatic conditions that have enabled species, particularly older lineages, to persist in specific ecological niches without the need for long-distance migration, as shown by phylogenetic studies of species persistence in stable environments (Crisp & Cook, 2013). This is particularly evident in areas with altitudinal gradients, where species can maintain stable conditions by shifting along these gradients (Rumpf et al., 2018). However, the complexity of species distribution patterns in eastern Australia suggests that other environmental factors may also play equally significant roles, particularly in complexes we have yet to investigate in-depth.

The interaction between various factors such as edaphic properties, geomorphology, and vegetation creates a dynamic system where no single factor dominates. While edaphic soil properties are well-established as influencing plant diversity and ecosystem dynamics (Hulshof & Spasojevic, 2020), the reciprocal role of vegetation, including its broader influence on nutrient cycling, soil retention, and geomorphology, remains understudied (Marston, 2010). Vegetation, for instance, has the capacity to influence geomorphology through root stabilisation and nutrient cycling, adding another layer of complexity to the factors shaping species distributions (Marston, 2010). Furthermore, disturbances such as historical grazing and fire regimes can alter erosion rates and reshape landscapes (Swanson, 1981). Fire regimes, in particular, have been shown to significantly influence species distributions in volcanic complexes such as Atherton (Ash, 1988). Thus, the feedback between vegetation and geomorphology depends strongly on each landscape's unique environmental history (Marston, 2010). As such, understanding species distributions across volcanic complexes requires an integrated view of many interacting factors. However, these critical refugia face imminent threat from the accelerating impacts of climate change, as rapidly increasing temperatures and shifting precipitation patterns are expected to destabilise the conditions that currently support range-restricted species (Harrison & Noss, 2017).

Broader Implications and Future Directions

The findings from this study align with the broader literature on volcanic complexes as refugia for biodiversity, reinforcing their role in supporting range-restricted and endemic species. Previous work by Reside et al. (2014) highlighted the importance of mountainous areas like Tweed and Tasmania as climate refugia, where stable conditions have allowed endemic species to persist. Our study extends this understanding by demonstrating how volcanic complexes along Australia’s entire eastern seaboard, spanning over 3000 km, form part of a larger biogeographic and ecological system. By examining these complexes at a finer spatial resolution, we were able to identify smaller, previously overlooked centres of endemism, and define four distinct types of ecological insularity. Our broader scope of Cenozoic volcanic complexes in Australia, which are almost exclusively found in eastern Australia, provides a more nuanced picture of how volcanic complexes function, both as refugia for climate-sensitive species and as dynamic landscapes shaped by various factors, including fire regimes (Clarke, 2002), soil properties and resource competition (Lambers et al., 2010).

The GWE analysis revealed that volcanic complexes are critical centres of endemism, often coinciding with bioregions of high phylogenetic endemism, such as Cape York Peninsula, Wet Tropics, and South Eastern Queensland (Kooyman et al., 2013). In contrast to earlier studies that used larger spatial resolutions, such as 1° grid cells by Crisp et al. (2001), this study employed a multiscale approach, at bioregion and sub-bioregional level. Our finer-scale approach (10 km) is particularly important because it allows for more precise identification of local areas of endemism, which might be overlooked at coarser resolutions. At this level, small but ecologically significant centres of endemism were detected, reinforcing the need for targeted conservation efforts in specific localities. For example, Atherton’s endemic centre spans the mafic volcanic complex, while the northern Wet Tropics' centre is situated on sedimentary units in the Daintree National Park. The separation of these centres of endemism by topographic corridors, such as the Black Mountain corridor, illustrates how landscape features influence species distribution (Crisp et al., 1995; Edwards et al., 2017).

Herbarium datasets used in this study, while extensive, are often biased due to uneven taxonomic and spatial sampling efforts (Daru et al., 2018). These biases highlight the need for more comprehensive sampling across volcanic complexes to better understand the full extent of species distributions and the role of these landscapes in preserving biodiversity. Moreover, the reliance on herbarium data means that certain fine-scale distribution patterns may remain underexplored, limiting the full scope of insights into the true extent of endemism within these volcanic complexes. Future research should continue to explore the interactions between climate, topography, and other environmental drivers in volcanic complexes, particularly as climate change and land-use pressures threaten to alter species distributions. Enhanced conservation efforts, including the identification and monitoring of key endemic species and developing region-specific recovery management plans will greatly improve their chance of survival into the future (Lavery et al., 2021). By understanding the multifactorial nature of insularity in volcanic landscapes, we can better protect the endemic species that rely on these fragile ecosystems because preserving these unique volcanic ecosystems is vital for maintaining biodiversity and ecological services crucial for human well-being (Molina-Venegas, 2021).

5 Conclusion

This study demonstrated that Cenozoic volcanic complexes in eastern Australia are crucial centres of endemism and ecological insularity. By identifying four distinct types of insular complexes, we provided new insights into how these volcanic landscapes function as biogeographic continental islands, supporting range-restricted species and fostering unique ecological dynamics. The interplay of climate, topography, and soil factors, rather than volcanic lithology alone, has been shown to drive species distributions across selected complexes. These findings underscore the importance of tailored conservation strategies that account for the complex and dynamic nature of these ecosystems.

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Table 1: Summary of volcanic complexes by insularity for species on volcanic complexes compared to occurrences on the surrounding sedimentary lithology matrix across 31 volcanic complexes in eastern Australia. Volcanic complexes are categorised based on the Area of occupancy (AOO) and extent of occurrence (EOO) of all species and species exclusive to the volcanic or sedimentary matrix. The table shows whether both AOO and EOO are smaller, larger, or varied (AOO larger, EOO smaller, or vice versa) than those in the surrounding matrix, highlighting the degree of insularity for each complex.

Species occurrence	**AOO and EOO Both Smaller Than Matrix**	**AOO and EOO Both Larger Than Matrix**	**AOO Larger, EOO Smaller Than Matrix**	**AOO Smaller, EOO Larger Than Matrix**
All species	Atherton Canobolas Comboyne Hillsborough Peak Range Snowy Mountains	Abercrombie Barrington Buckland Chudleigh Dubbo Liverpool Range McBride Monaro New England Newer Volcanics Nulla Older Volcanics Piebald Southern Highlands Sturgeon	Bunya Main Range Nandewar Nebo Tasmania Tweed Walcha Warrumbungle	Glass House Mountains, Springsure
Exclusive species	Abercrombie Atherton Barrington Buckland Canobolas Comboyne Hillsborough Main Range McBride New England Older Volcanics Peak Range Southern Highlands Sturgeon Tweed Walcha Warrumbungle	Chudleigh Glass House Mountains Liverpool Range Newer Volcanics Nulla Piebald	Bunya, Nandewar Nebo Snowy Mountains	Dubbo Monaro Springsure Tasmania

Table 2: The top three predictors of area f occupancy and extent of occurrence for volcanic complexes with high insularity in eastern Australia identified by random forest models. The predictors include topographic, climatic, vegetation community and soil variables. Climatic variables include present (1981-2010) (Karger et al., 2017), Last Glacial Maximum (LGM; 21,000 years ago) (Karger et al., 2023), and the differences (Δ) between the two datasets taken as an indicator for climate stability for identifying refugia in mafic and bimodal (BM; both mafic and felsic) volcanic complexes.

Volcanic Complex	**Lithology type**	**Area Of Occupancy**	**Extent Of Occurrence**
Atherton	Mafic	Δ Annual Precipitation	Δ Precipitation Warmest Quarter
		Δ Precipitation of Coldest Quarter	Δ Annual Precipitation
		Available phosphorus 60-100 cm	Soil organic carbon 0-30cm
Peak Range	Mafic	Present Precipitation Wettest Quarter	Terrain ruggedness index
		Soil organic carbon 60-100 cm	Soil organic carbon 60-100 cm
		Terrain ruggedness index	Δ Mean Temperature Driest Quarter
Canobolas	BM	LGM Max Temperature of Warmest Month	LGM Annual Precipitation
		Δ Temperature Annual Range	LGM Precipitation of Warmest Quarter
		LGM Precipitation of Driest Quarter	Δ Mean Temperature of Wettest Quarter
Comboyne	BM	Δ Mean Diurnal Range	Δ Mean Temperature Driest Quarter
		LGM Max Temperature of Warmest Month	Δ Temperature Annual Range
		Δ Mean Temperature Driest Quarter	LGM Max Temperature of Warmest Month
Tweed	BM	Δ Annual Precipitation	LGM Precipitation of Wettest Quarter
		LGM Precipitation of Wettest Quarter	Δ Annual Precipitation
		Δ Mean Diurnal Range	Δ Precipitation of Coldest Quarter

Figure 1: Map of Cenozoic volcanic lithologies in eastern Australia, classified into three provinces by Wellman and McDougall (1974): Central Volcanoes (red), Basalt Lava Fields (blue), and Leucitite Suite (purple). Central Volcanoes consist of volcanic complexes with predominantly basaltic but also felsic lava flows or intrusions. Basalt Lava Fields are extensive and predominantly basaltic regions formed from diffuse dykes and pipe swarms, often featuring small scoria cones and maars. The Leucitite Suite comprises high-potassium mafic rocks with leucitite intrusions, distinct from other volcanic areas in eastern Australia. The provinces are drawn following Johnson & Wellman (1989). Red arrows show the proposed volcanic hotspot tracks following Davies et al. (2015).

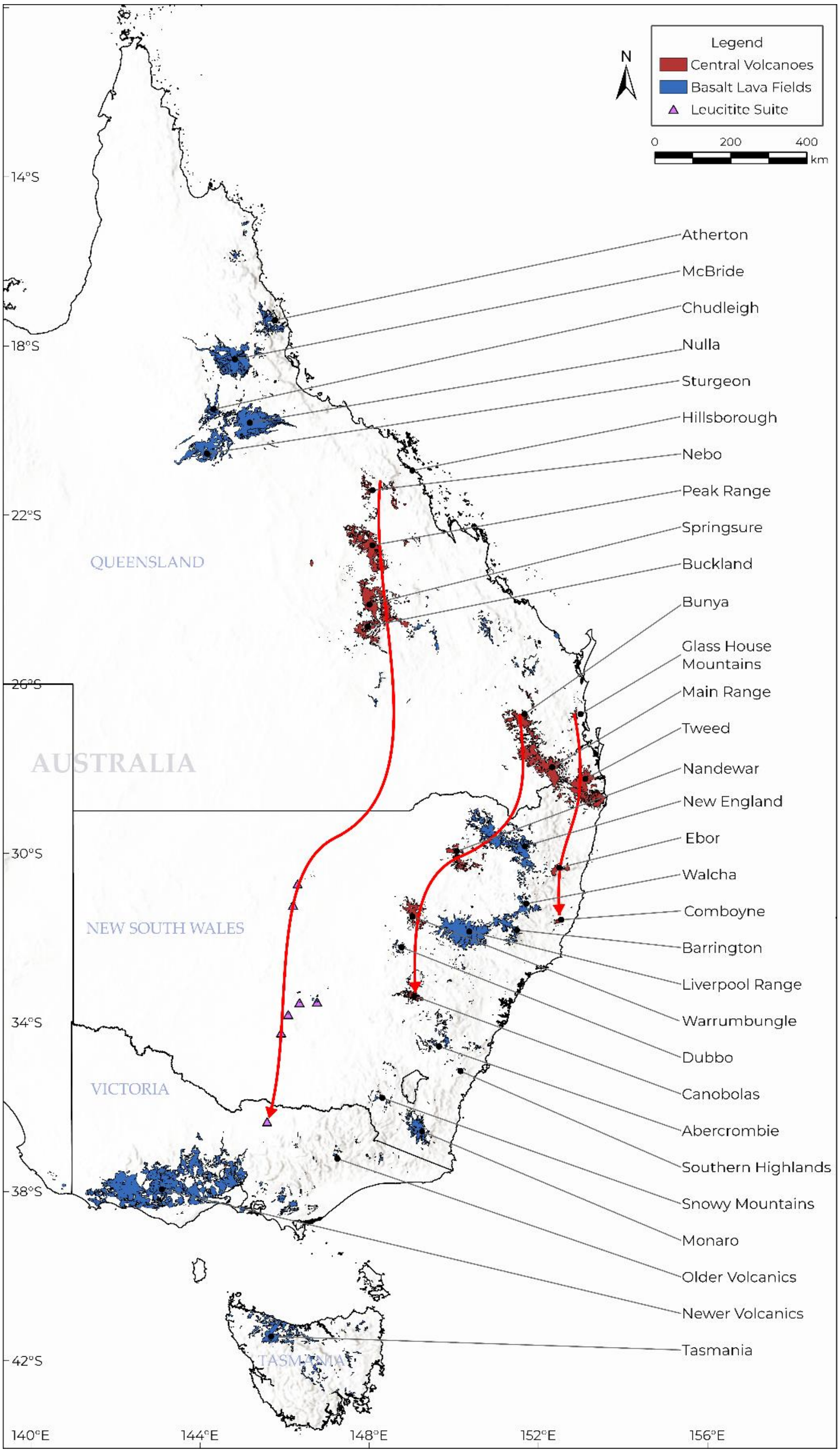

Legend
Central Volcanoes
Basalt Lava Fields
Leucitite Suite
N
0
200
400
km
14°S
18°S
22°S
26°S
30°S
34°S
38°S
42°S
140°E
144°E
148°E
152°E
156°E
QUEENSLAND
AUSTRALIA
NEW SOUTH WALES
VICTORIA
TASMANIA
Atherton
McBride
Chudleigh
Nulla
Sturgeon
Hillsborough
Nebo
Peak Range
Springsure
Buckland
Bunya
Glass House Mountains
Main Range
Tweed
Nandewar
New England
Ebor
Walcha
Comboyne
Barrington
Liverpool Range
Warrumbungle
Dubbo
Canobolas
Abercrombie
Southern Highlands
Snowy Mountains
Monaro
Older Volcanics
Newer Volcanics
Tasmania

Figure 2: Summary statistics of the extent of occurrence (EOO) and area of occupancy (AOO) in km² for species associated with different lithology classes. The number of endemic species per lithology class (n) and the distribution of EOO and AOO values are displayed in violin plots, which illustrate the density distribution of these values. Median values are represented within the boxplots and labelled for each class. Panels a) and b) show the EOO and AOO, respectively, for species found exclusively within each lithology class. Panels c) and d) depict the EOO and AOO, respectively, for species predominantly found (≥95% of occurrences) within a single lithology class. The lithology classes are Intrusive, Sedimentary, Volcanic-Sedimentary Mix and Volcanic.

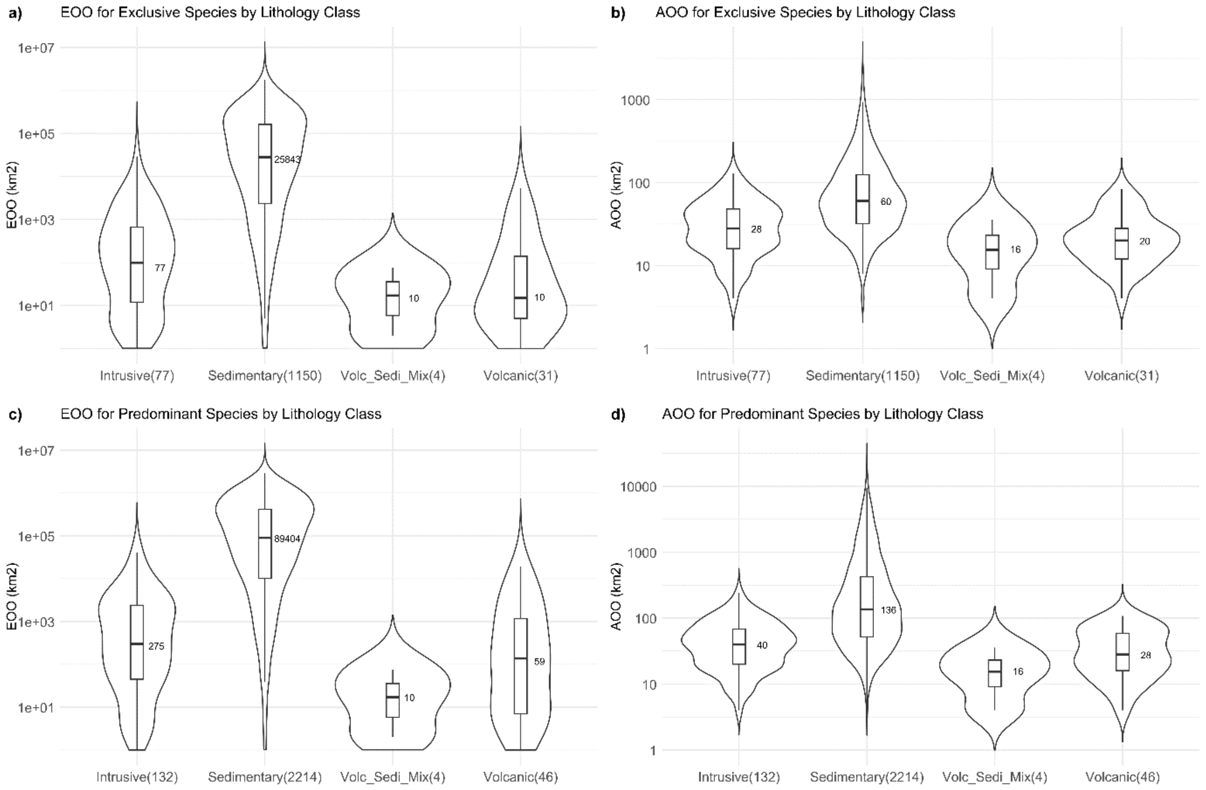


Figure 3: Georeferenced Weighted Endemism (GWE) across the study area with A) GWE values indicating the endemicity of each grid cell (10 km) calculated as the sum of the inverse of the extent of occurrence of species occurring within the cell, B) Species richness, as the total number of unique species found in each cell, C) results of the non-parametric significance test, showing areas where GWE scores are statistically significant (yellow cells), and D) outliers of GWE scores, marked as areas where the values exceed 1.5 times the interquartile range of the null distribution given the species richness for each grid cell. The outliers are categorised as either a lower outlier (-1), non-outlier (0), or upper outlier (1).

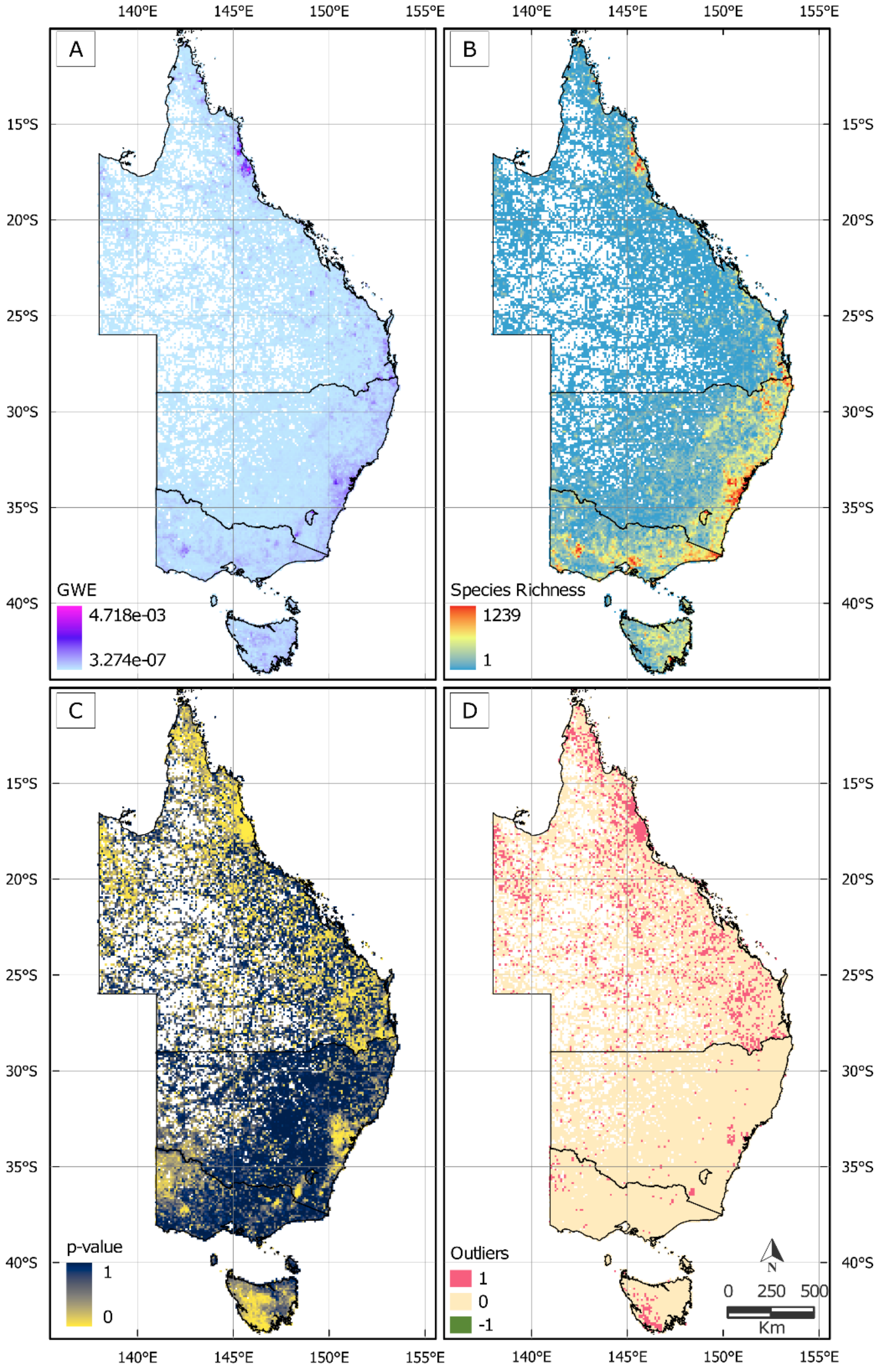


Figure 4: Georeferenced Weighted Endemism (GWE) results, highlighting centres of endemism within various volcanic complexes (VC) across eastern Australia; with A) high endemism in Atherton and moderate endemism in McBride, B) high endemism in Tweed, Main Range and Glass House Mountains, C) high endemism in Sydney (most not on Cenozoic volcanic lithologies), D) moderate endemism in Nandewar, Warrumbungle and Barrington, and E) high endemism in Hobart and Central Highlands in Tasmania.

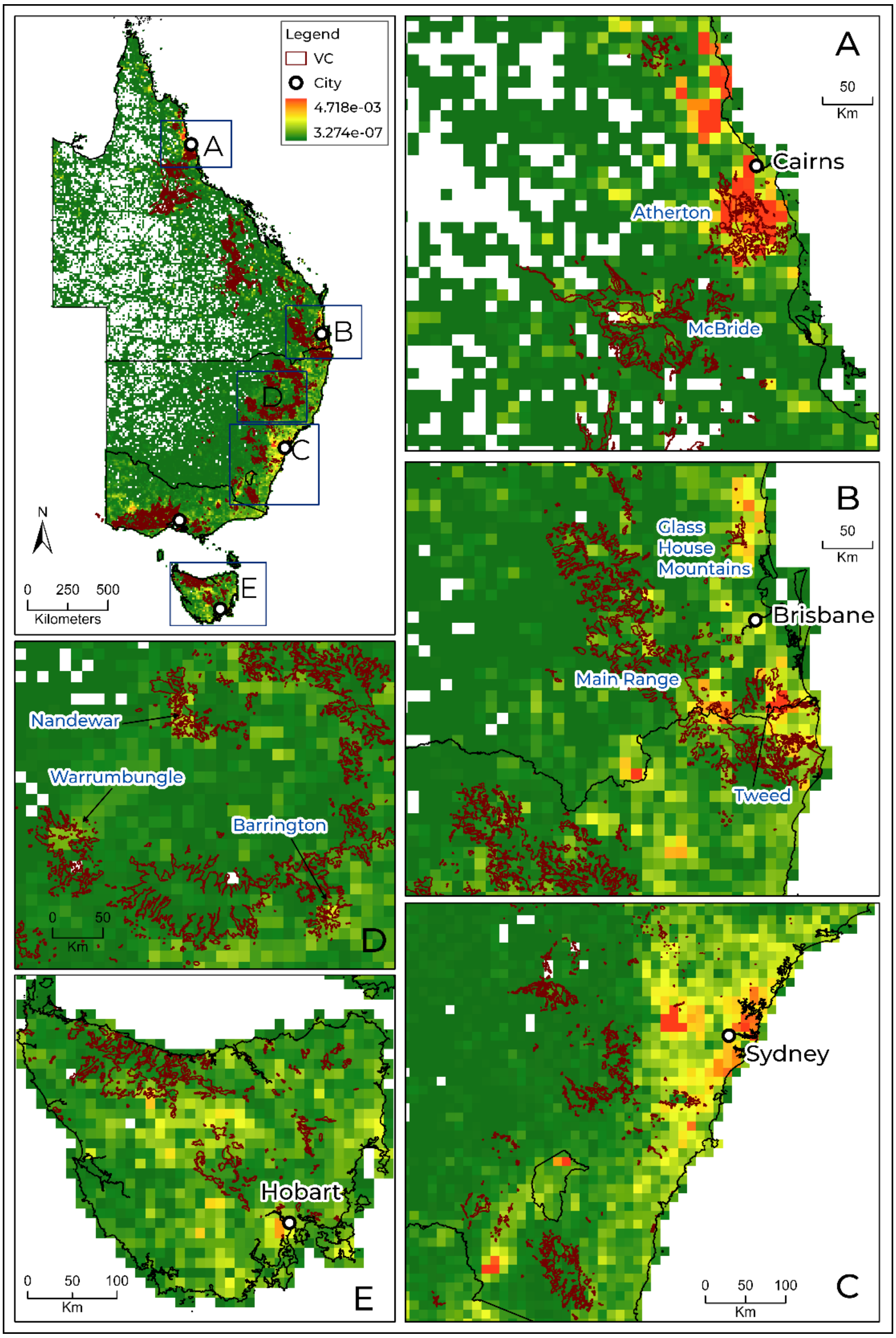
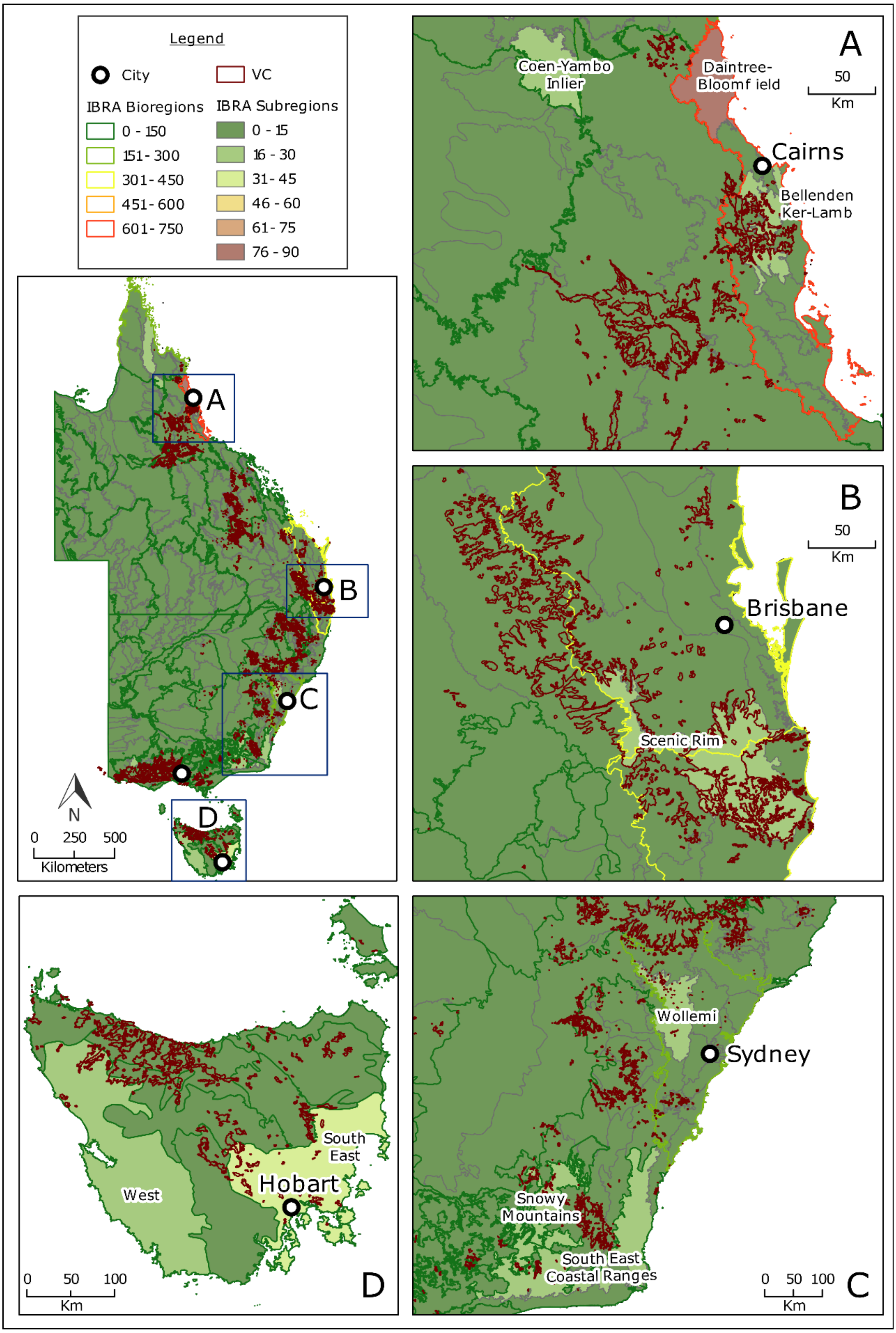


Figure 5: Distribution of endemic species relative to volcanic complexes (VC) within IBRA Bioregions and Sub-bioregions in eastern Australia. A species is considered endemic if 95% or more of its occurrence records fall within a single bioregion or sub-bioregion. Key regions include: A) The Wet Tropics (WET) Bioregion, with most endemic species located in the Daintree-Bloomfield and Bellenden Ker-Lamb Ranges sub-bioregions. B) South Eastern Queensland (SEQ) Bioregion, with endemic species concentrated in the Scenic Rim sub-bioregion. C) Sydney Basin (SYB) Bioregion, has most of it’s endemic in the Wollemi sub-bioregion. The Australian Alps Bioregion is concentrated in the Snowy Mountains sub-bioregion, and the South East Corner Bioregion is mainly in the South East Coastal Ranges sub-bioregion. D) Tasmania Bioregion, with endemic species primarily in the West and South East sub-bioregions.


Legend
City
VC
IBRA Bioregions
0 - 150
151 - 300
301 - 450
451 - 600
601 - 750
IBRA Subregions
0 - 15
16 - 30
31 - 45
46 - 60
61 - 75
76 - 90
A
B
C
D
N
0 250 500
Kilometers
Coen-Yambo Inlier
Daintree-Bloomf ield
50 Km
Cairns
Bellenden Ker-Lamb
Brisbane
Scenic Rim
South East
Hobart
West
0 50 100 Km
Wollemi
Sydney
Snowy Mountains
South East Coastal Ranges