Biogeographical regions and phytogeography of the eucalypts

Carlos E. González-Orozco[1]*, Andrew H. Thornhill[1], Nunzio Knerr[1], Shawn Laffan[2] and Joseph T. Miller[1]

[1]*Centre for Australian National Biodiversity Research, CSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia,* [2]*School of Biological Earth and Environmental Sciences, University of New South Wales, Kensington, Sydney, NSW 2052, Australia*

ABSTRACT

Aim To map spatial patterns of species richness, species endemism and species turnover of the eucalypts; to propose a biogeographical regionalization of eucalypts based on species turnover; and to identify the environmental correlates of these patterns.

Location Australia and Malesia.

Methods We analysed 798 eucalypt species (*Angophora, Corymbia* and *Eucalyptus*) with distributions across Australia and Malesia using square cells with a resolution of 100×100 km. Species richness, endemism and species turnover were calculated. Phytogeographical regions were identified using an agglomerative cluster analysis derived from a matrix of pairwise Simpson's beta (β_{sim}) dissimilarity values. Eleven environmental variables were used to analyse the environmental correlates of species turnover. Non-metric multidimensional scaling (NMDS) of the β_{sim}, Getis-Ord Gi* hotspot spatial statistics and an ordination of the β_{sim} -NMDS were used to investigate the environmental drivers at the continental level and for each of the phytogeographical regions.

Results We identified three centres of species richness and fourteen of endemism, of which several are newly identified. The main centres of species richness agree with previous studies. Six major eucalypt phytogeographical regions are proposed based on the species turnover: monsoon, tropical/subtropical, south-east, south-west, Eremaean north and Eremaean south. These findings are supported by significant environmental differences of the NMDS vectors and the Gi* statistics. The environmental drivers of species turnover are broadly consistent with the continental patterns of summer and winter rainfall below and above the Tropic of Capricorn.

Main conclusions The proposed phytogeographical regions are similar to the Australian biomes. Climate is the main driver of the phytogeographical regions, varying from region to region. Comprehensive bioregionalization frameworks and phytogeography updates, as proposed here, are fundamental for enhancing our understanding of the spatial distribution of biodiversity and therefore benefit global biogeography and help planners to identify regions of high conservation relevance.

Keywords

Australia, biomes, endemism, environmental drivers, eucalypts, NMDS, regionalization, species richness, species turnover β_{sim}.

*Correspondence: Carlos E. González-Orozco, Institute for Applied Ecology and Collaborative Research Network for Murray-Darling Basin Futures, University of Canberra, Canberra, ACT 2601, Australia. E-mail: carlos.gonzalez-orozco@canberra.edu.au

INTRODUCTION

The eucalypts, the most abundant group of canopy woody plants in the Australian continent, are comprised of three genera: *Angophora* (Smith), *Corymbia* (K.D. Hill & L.A.S.

Johnson) and *Eucalyptus* (L'Hér.) (Brooker *et al.*, 2006). The eucalypts consist of around 800 species (894 taxa) with a high level of taxonomic (Nicolle, 1997, 2006; Brooker, 2000; Dorothy *et al.*, 2002) and phylogenetic diversity (Brooker & Kleining, 1983; Ladiges *et al.*, 1995, 2003; Ladiges, 1997).

The most recent study of distribution patterns (Gill *et al.*, 1985) mapped species richness, endemism and general bioregions for *Eucalyptus* and *Corymbia* excluding *Angophora*. Since then an additional 250–300 species have been named and *Corymbia* has been elevated to a genus (Hill & Johnson, 1995; Brooker, 2000; Brooker *et al.*, 2006). There has also been a considerable increase in the availability of digitized herbarium records with geographical coordinates and allied environmental datasets, which can be used to explore species distribution patterns. All these elements combined provide an important opportunity to produce a comprehensive and updated analysis of their phytogeography.

Bioregionalizations are an useful approach to the understanding of patterns of biodiversity (Wallace, 1894). For example, they have been successfully applied to delineate zoogeographical regions of the world (Kreft & Jetz, 2010; Holt *et al.*, 2012). Bioregionalizations provide a way to identify units of ecological, evolutionary and historical relevance, enhancing our understanding of the spatial distribution of a biota (Morrone & Crisci, 1995). Also, by grouping the bioregions into clusters of meaningful geographical units, relationships among regions can be revealed. This is essential to reconstruct the natural history of a continent. Consequently, these aspects are important for future management of biodiversity and ultimately conservation planning.

The Interim Biogeographic Regionalisation of Australia (IBRA; Thackway & Cresswell, 1995) is a comprehensive bioregionalization that integrates many data types, including expert opinion and political boundaries, making it a challenge to interpret biologically. In contrast, climate centred approaches, based on environmental variables, gross primary productivity and remote sensing data, but no biological factors, were explored by Mackey *et al.* (2008) and Hutchinson *et al.* (2005). A consistent taxonomy of bioregionalization frameworks would greatly help the research field (Ebach, 2012).

We use Simpson's beta dissimilarity metric to generate a bioregionalization of the eucalypt phytogeographical regions in Australia and Malesia, and then assess the relationships of the phytogeographical regions to the environment. Specifically our goals were to: (1) map spatial patterns of species richness, species endemism and species turnover, (2) propose a biogeographical regionalization of eucalypts based on species turnover and (3) assess the relationship of the phytogeographical regions to environment. These data were compared with other spatial analyses of the Australian flora and together allow the testing of previous biogeographical classifications.

METHODS

Taxonomic and spatial dataset

Angophora, *Corymbia* and *Eucalyptus* species records were extracted from the Australian Virtual Herbarium database (AVH; CHAH, 2010). The point records are given Appendix S5. Australian collections were curated to the accepted taxonomy of the Australian Plant Census (Lepschi & Monro, 2011). We excluded hybrids and used varieties and subspecies data at the species level to reduce taxonomic uncertainty. Species distributions outside of Australia and Malesia were not included if they were not available in the AVH.

Spatial errors were identified, and taxonomic corrections were applied using the ArcMap and Google Refine software, respectively. Records without a geographical location were deleted, as were records located in the ocean or outside continental Australia and the Malesian region. The geographical range of each species was corrected manually according to the species distributions in the Euclid database (Brooker *et al.*, 2006) to exclude cultivated or naturalized collections. The geographical coordinates of the remaining 219,799 records were projected into a Lambert's conic conformal coordinate system to avoid the latitudinal biases of geographical coordinate systems, and then aggregated to 100 km × 100 km grid cells (906 in total) using the Biodiverse software, version 0.18 (Laffan *et al.*, 2010). This grid cell size was chosen to be consistent with Gill *et al.* (1985) and with González-Orozco *et al.* (2013).

Environmental dataset

A correlation matrix, available through the spatial portal of the Atlas of Living Australia (ALA; htpp://www.ala.org.au/), was used to select 11 environmental variables, which represented different environmental traits and contained minimal correlation (Table 1). We also selected some environmental variables based on previous hypotheses of their effectiveness in predicting the distribution of species in Australia (Austin *et al.*, 1994; González-Orozco *et al.*, 2013). The climatic variables are described in Houlder (2000) and Hutchinson *et al.* (2000), who developed the layers using *ANUCLIM* 6.1. The soil layers were obtained from the National Land & Water Resources Audit (ALWARA, 2002; Johnston *et al.*, 2003). The spatial resolution of the layers was 1 km (*c.* 0.01°). The environmental layers were reprojected into the same Lambert's conic conformal coordinate system as the species data and also aggregated to 100 km × 100 km grid cells using Biodiverse. For each environmental variable, we calculated the mean, standard deviation, coefficient of variation, minimum and maximum values of the set of 1 km grid cells within each 100 km grid cell, again using Biodiverse.

Species richness and endemism

Species richness (SR), weighted endemism (WE) and corrected weighted endemism (CWE) were calculated in the Biodiverse software version 0.18 (Crisp *et al.*, 2001; Laffan *et al.*, 2010, 2013) for each 100 km × 100 km grid cell. CWE is a relative measure of endemism and is essentially a function of range restriction. It can be interpreted as the degree to which ranges of species found in the grid cell are, on average, restricted to that grid cell (Laffan & Crisp, 2003). Once the species richness and endemism scores were calculated for all

Table 1 Environmental variables used in our analyses.

Environmental variable	Description
Annual precipitation	Monthly precipitation estimates (mm)
Annual mean temperature	The mean of the week's maximum and minimum temperature (°C)
Annual mean radiation	The mean of all the weekly radiation estimates (Mj m^{-2} day^{-1})
Precipitation of coldest quarter	Total precipitation over the coldest period of the year (mm)
Radiation seasonality	Standard deviation of the weekly radiation estimates expressed as a percentage of the annual mean (Mj m^{-2} day^{-1})
Precipitation seasonality	Standard deviation of the weekly precipitation estimates expressed as a percentage of the annual mean (mm)
Temperature seasonality	Standard deviation of the weekly mean temperatures estimates expressed as a percentage of the annual mean (°C)
Ridge top flatness	Metric of the topographic flatness derived from a 9 arc-second resolution raster digital elevation model (dimensionless; Gallant & Dowling, 2003)
Rock grain size	Lithological property of the bedrocks related to the mean grain size (0–10 units)
Percentage of sand	Content of sand (%) in the top 30 cm of soil layer estimated from soil maps at a resolution of 1 km (%)
Percentage of clay	Content of clay (%) in the top 30 cm of soil layer estimated from soil maps at a resolution of 1 km (%)

grid cells, we defined centres of species richness and endemism by selecting those grid cells with the highest 1% of scores (Orme et al., 2005; González-Orozco et al., 2011).

Species turnover

A matrix of Simpson's beta (β_{sim}) species turnover was generated for all pairwise grid cell combinations (Tuomisto, 2010). Simpson's beta was used because it reduces the effect of any species richness imbalance between locations.

$$\beta sim_{i,j} = 1 - \frac{a}{a + \min(b, c)}$$

where a refers to the number of species common to cells i and j, b is the number found in cell i but not cell j, and c is the number found in cell j but not cell i. A low β_{sim} value indicates that many taxa are shared between two grid cells (low dissimilarity) and a high β_{sim} means a small number of shared taxa (high dissimilarity).

Cluster analysis

The β_{sim} pairwise distance matrix was used in an agglomerative cluster analysis to generate a WPGMA (weighted

pair-group method using arithmetic averages) hierarchical cluster in BIODIVERSE. WPGMA weights the contributions of clusters by the number of terminal nodes (data set cells) they contain, ensuring each cell contributes equally to each merger of which it is a part. Its performance was determined to be as successful as UPGMA in Kreft & Jetz (2010).

We implemented a tie breaker approach such that, when more than one pair of clusters had the minimum turnover score and thus could be merged, the algorithm selected the pair that maximized the corrected weighted endemism score in the cluster (Crisp et al., 2001; Laffan & Crisp, 2003). This approach guarantees a stable solution that is replicated each time the analysis is run, as well as increasing the degree of endemism and thus the spatial compactness of the resultant bioregions. We identified the phytogeographical regions from the clusters based on two criteria: (1) a phytogeographical region is preferably represented by a group of contiguous, or near-contiguous, grid cells, (2) each cluster that represents a phytogeographical region needs to be clearly separated from its children or parent.

Relative Environmental Turnover

Relative environmental turnover (RET) was applied to understand the relationship of environmental variables to the phytogeographical regions estimated using species turnover, as first tested with the Australian genus Acacia (González-Orozco et al., 2013). Previous studies used the term environmental turnover to explore rates of change of dissimilarity in vertebrates and their relationship to environment depending on the geographical distance (Buckley & Jetz, 2008). RET differs from other studies because it contains two types of analyses: ordinations of the β_{sim} with the environmental variables and the grid cell-based Getis-Ord Gi* hotspot statistic.

For the ordination analyses, a non-metric multidimensional scaling (NMDS) ordination was generated using the β_{sim} values. We used NMDS because it is an unconstrained metric that assumes neither normally distributed variables nor linear relationships between variables. This approach allows us to obtain a dimensionless ordination diagram with axes that can be interpreted in terms of an environmental gradient. More traditional methods such as principal component analyses (PCA) were not applied because they assume the data follow a linear normal distribution. Mean values for each of the grid cells were extracted from the 100 km environmental layers. We used the R statistical software (R Development Core Team, 2005) to produce the β_{sim} values in a matrix format. We then matched the records between the β_{sim} dissimilarity matrix and the mean per cell values of the environmental datasets (see Appendix S2 for heat maps of the environmental variables). The function 'metaMDS' of the vegan package (Oksanen et al., 2012) was then used to generate the ordination. The β_{sim} values were overlaid onto the ordination and fitted with the environmental variable matrix using the vector fitting of the envfit function from the vegan package. The environmental variables that best

explained the patterns of turnover were then displayed as vectors only for those cases with high predictability ($P < 0.001$), assessed using 999 permutations. The stress values of the *envfit* results were used to estimate the efficiency of the NMDS ordinations. The environmental analyses excluded the Malesian region because most environmental variables were not available at an appropriate resolution for that region.

The values of grid cells along the first and second axes of the NMDS ordination of β_{sim} distances were extracted and mapped in ArcMap. The geographical rate of change of each axis was calculated using the slope tool in ArcGIS. Those locations with steep slope values correspond with rapid changes (breaks) in the geographical distributions of turnover.

The Getis-Ord Gi* hotspot statistic (Laffan, 2002; Külheim et al., 2011) was calculated using BIODIVERSE to assess whether the environmental values within each phytogeographical region were significantly different from those for the Australian continent as a whole, where each region was represented by its set of 100 km × 100 km cells. The Gi* statistic is expressed as a z-score indicating the degree to which the values of a subset of grid cells, in this case the cells comprising a cluster, are greater or less than the mean of the dataset. Those clusters with Gi* values >2 or <−2 represent sets of cells that have environmental values significantly different from expected ($P < 0.05$).

RESULTS

Species richness and endemism

The most species rich and endemic regions of eucalypts were located south of the Tropic of Capricorn. We identified three main centres of species richness (Fig. 1a). Six of the ten grid cells with the highest species richness scores (86–116 species per grid cell) were located in the south-east coastal province of the Southwest Floristic Region of Western Australia (location 1 in Fig. 1a). The remaining four of the ten centres (richness scores from 86 to 92) were located in south-eastern Australia. The New South Wales and Queensland border (location 3 in Fig. 1a) has not been previously identified as a centre of eucalypt species richness, although the general region was recognized as a centre of species richness for the Australian flora (Crisp et al., 2001).

Fourteen centres of high eucalypt endemism were identified (Fig 1b), with the highest scores (between 0.1 and 0.5) being located in Western Australia and East Timor. Five of these endemism centres are in eastern Australia (6, 9, 10, 11 and 12 in Fig. 1b) and were not identified by Crisp et al. (2001) as being among the 12 endemic areas of the Australian flora.

Phytogeographical regions

Seven eucalypt phytogeographical regions are proposed, of which six are in continental Australia and one comprises the

islands to its north (Fig. 2a). There are two small clusters in the Malesian islands: one in East Timor and the second further east including part of Indonesia, East Timor and Papua New Guinea, all of which have endemic eucalypt species. The remainder of the Malesian region clusters with larger Australian regions. One cluster differentiates the south-eastern Australia region from the rest of the continent (Fig 2b).

The dendogram branch lengths (Table 2) for each of the geographical clusters (Fig. 3) show Australia is subdivided into six major phytogeographical regions (A–F). The Eremaean north region is subdivided into four subregions, where the Pilbara (a) is most similar to western coastal (b) whereas central (c) is most similar to the Eastern (d) (See [(a,b) (c,d)] in Fig. 3A). The monsoon phytogeographical region is composed of mainland Australia and Malesian subregions, where the Top End/Malesia subregion (a) is most dissimilar to the rest of the subregions (See [(a) (b,c,d)] in Fig. 3B). The inland monsoon subregions are divided east-west in three subregions: east (b), central (c) and west (d). The tropical/subtropical region is an independent cluster related to the northern regions of the monsoon and the Eremaean north (See [(a) (b,c)] in Fig. 3C). This region has a strong north to south pattern with Cape York (a) to the north and a southern coastal cluster, which can be further separated into Queensland Central (b) and New South Wales south (c) subregions.

The Eremaean south and the south-west phytogeographical regions form a single cluster separate from the monsoon, Eremaean north and tropical/subtropical regions. While the branch combining the two areas is short, the branches supporting Eremaean south and the south-west are longer. We recognize these two eucalypt phytogeographical regions based on long nested branches. The south-west region is divided into south and west subregions (see [(a) (b,c)] in Fig. 3D). The Eremaean south region is subdivided into two subregions that stretch from east to west (See [(a,b) (c,d)] in Fig. 3E). The most eastern/central subregion further subdivides into a southern Murray-Darling Basin subregion (a) and a subregion along the Nullarbor coastal plain (b) whereas western subregions (c–d) of inland and coastal areas connect with the south-west region. The south-east region is subdivided into an alpine (a) subregion and a Tasmanian/ southern Victorian subregion (See [(a) (b,c)] in Fig. 3F). The southern portion subdivides into Tasmanian (b) and south-eastern mainland (c) subregions.

Relative environmental turnover (RET)

The geographical surface of the first NMDS axis indicates a major geographical break oriented north-west to east across the continent (Fig. 4a, see also the red line in Fig. 4c). This break is aligned with the summer–winter rainfall line defined by Burbidge (1960). The pattern produced by the second axis (Fig. 4b) matches the division of arid central Australia, which has less eucalypt diversity, and the mesic zone on the coastal regions of eastern Australia. Areas noted as having
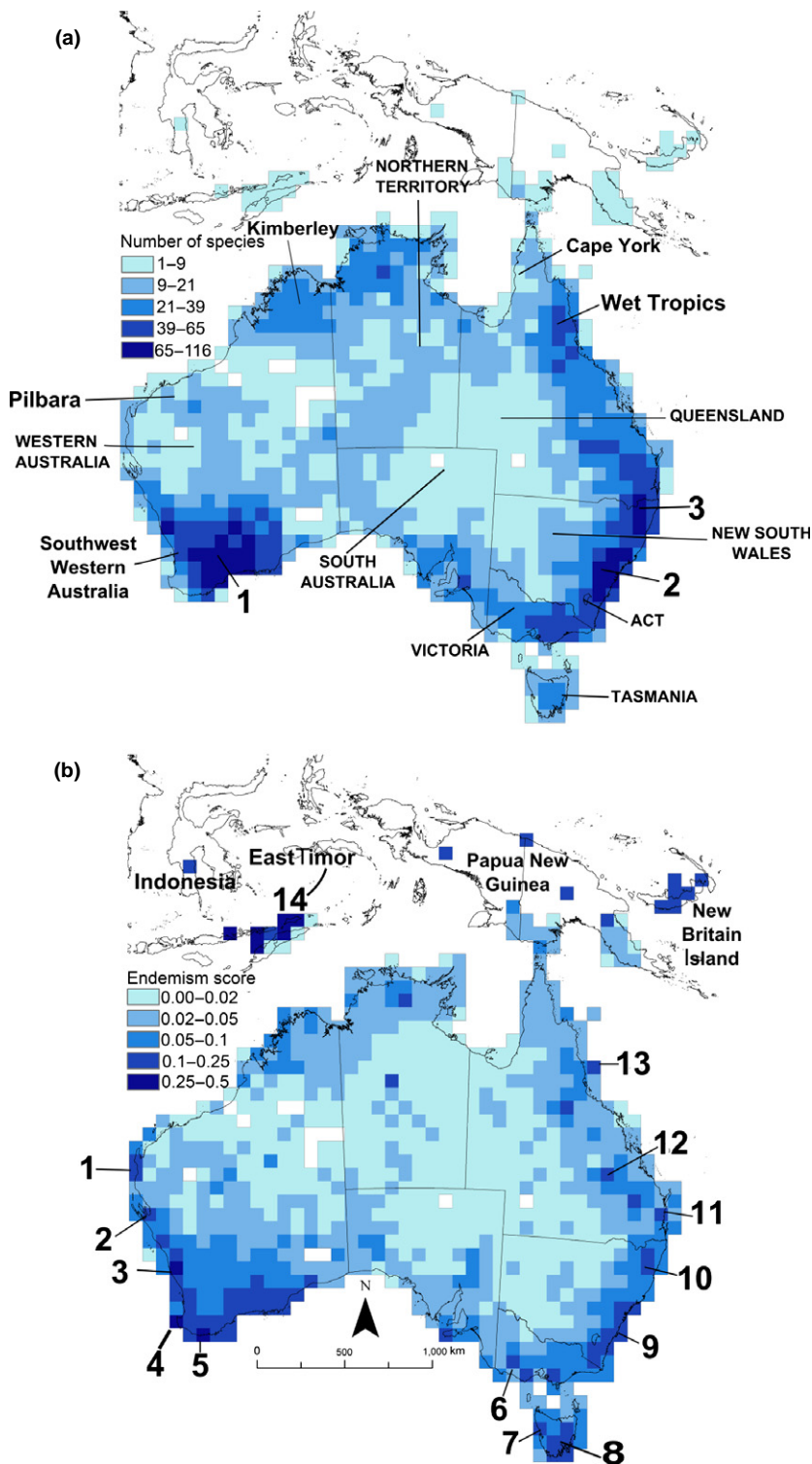
(a)

(b)

Figure 1 Maps of species richness (a) and endemism (b) for eucalypts in Australia and Malesia. Numbers in the maps are referred to in the text.

high slope values are regions with abrupt changes of species turnover and are inferred turnover breaks. For example, the major break we found is detected by NMDS1 (red line in Fig. 4c), and follows the subregion boundaries (Fig. 3). No major pattern is found for NMDS2, but ten small inferred turnover break areas are scattered across the continent (Fig. 4d). Of these, area 1 is a known barrier for the Wet

Tropics, area 2 corresponds to the MacPherson/MacLeay overlap zone between NSW and Queensland east coast, area 4 corresponds with the Murray and Gippsland Basin barriers, and area 10 reflects the known barrier of the Nullarbor Plain of southern Australia.

A low stress value (0.1016) suggests a good fit of the environmental data to the β_{sim} clusters in the ordination model
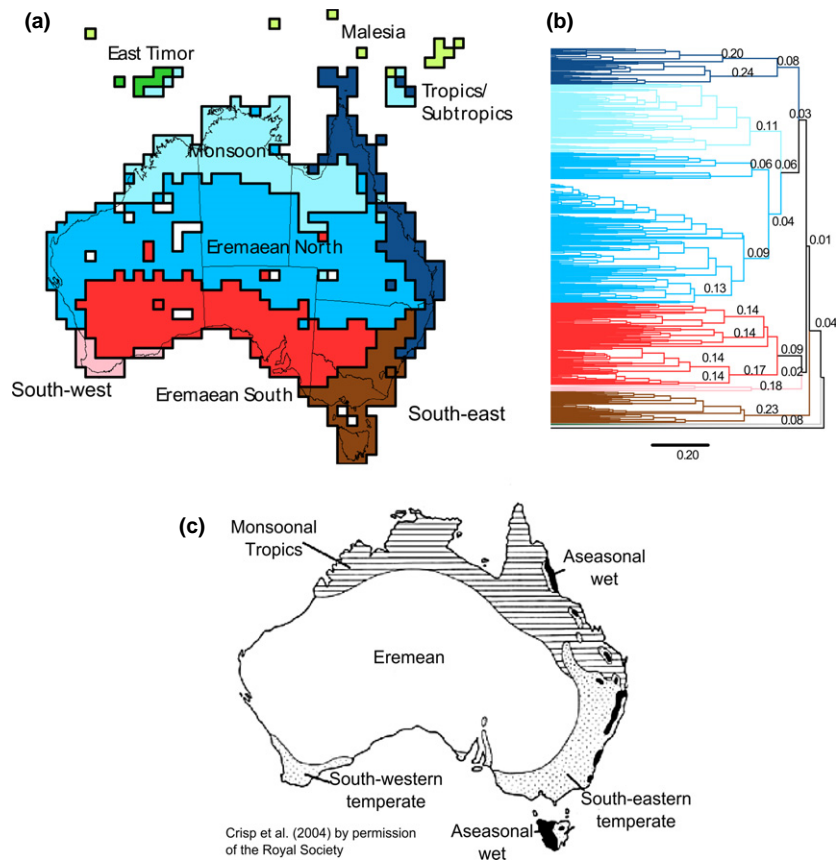
Figure 2 (a) Map of the seven eucalypt phytogeographical regions, (b) corresponding cluster dendogram and (c) the biomes of Australia according to Crisp *et al.* (2004). Map regions are coloured based on relationship in the corresponding dendogram. For example the blue regions for a higher level cluster as do the red colours. Figure 2a contains two green clusters in Malesia. These two clusters subtend the rest of the dendogram (2b) and are shown in black and grey for clarity.

(Fig. 5). With the exception of clay content, all variables were significantly ($P < 0.001$) correlated with β_{sim}. For example, the values towards the northern areas of monsoonal Australia correspond with the points located in the top left corner of the plot (indicated by the North arrow). The vectors for annual precipitation and precipitation during winter vectors correlate with species turnover towards the east and north-west of Australia. Vectors for temperature seasonality, annual mean radiation, topography, sand content and lithology correlate with species turnover towards the west and south-west of Australia. Vectors for annual mean temperature and annual mean radiation vectors correlate with species turnover towards the western parts of the monsoon region as well as the central Australian deserts located in the eastern part of the Eremaean north region. Vectors for precipitation during the coldest quarter and radiation seasonality were highly correlated with the southern regions.

The results of the gridded approach, where the effects of 11 environmental variables were tested in each of the eucalypt bioregions, are shown in Table 4. A value >2 or <−2 indicates that the values of an environmental variable in that floristic region are, collectively, significantly different from the study region as a whole. Overall, climate variables such as precipitation and temperature appear more important for explaining the turnover patterns of the eucalypt phytogeographical regions than are non-climatic variables such as soil and topography. However, there is some degree of variability from region to region. For example, precipitation seasonality is the main driver for the monsoon region, while precipitation during coldest quarter of the year is the main driver for the south-eastern region. Temperature seasonality is the main driver for the Eremaean north region, meaning that monthly variation in temperature correlates well with species turnover in the drier and hotter areas north of the Tropic of Capricorn. Interestingly, precipitation seasonality represented as winter rainfall (south of the Tropic of Capricorn) becomes the main driver for the Eremaean south region, meaning that rainfall patterns between June and August play a determinant role. As expected, the main driver of the tropical and subtropical north-eastern and eastern regions is annual mean precipitation. The species turnover in the temperate regions of south-east and south-west Australia is highly correlated with the amount of precipitation during winter months. The results of the gridded approach tested on each of the eucalypt subregions are given in Table S3 of Appendix S3.

Table 2 Values of branch length for clusters of floristic regions and subregions of Australian eucalypts.

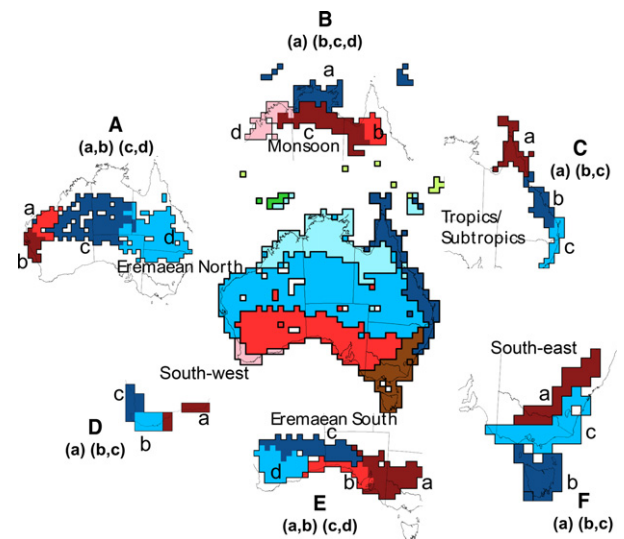| Eucalypt phytogeographical regions	Geographic subdivisions	Branch length to parent (brackets refer to subregions labels in Fig. 3)
Malesia	Top End/Malesia	0.04
	Monsoonal Belt	0.08
South-east	(Major split)	0.23
	Alpine	0.21 (a)
	Tasmanian/southern Victoria	0.15
	Tasmanian	0.27 (b)
	South-eastern mainland	0.03 (c)
Eremaean south/south-west	(Major split)	0.01/0.02
	Eremaean south:	0.03
	Southern MDB	0.14 (a)
	Nullarbor Plain	0.18 (b)
	Northern	0.14 (c)
	Southern	0.14 (d)
	South-west:	0.18
	Eastern/Central	0.40 (a)
	Western (Southern)	0.21 (b)
	Western (Northern)	0.53 (c)
Tropical/Subtropical	(Major split)	0.03/0.08
	Tropical:	0.20 (a)
	Cape York	0.17 (b)
	QLD North	0.24
	Subtropical:	0.34 (c)
	NSW South	
Monsoon/Eremaean north	(Major split)	0.06
	Monsoon:	0.11
	Malesia	0.16 (a)
	East	0.16 (b)
	Central	0.06 (c)
	West	0.12 (d)
	Eremaean north:	0.04
	West	0.06
	Western- Pilbara	0.13 (a)
	Western- Coastal	0.15 (b)
	Central eastern	0.10
	Central	0.07 (c)
	Eastern	0.04 (d)

Figure 3 Map of the eucalypt phytogeographical regions and their respective subregions. Regions are denoted in upper case letters: A = Eremaean north; B = monsoon; C = Tropical/subtropical; D = south-west; E = Eremaean south; F = south-east. Subregions are denoted in the parenthetical notation using lower case (see Table 3 for corresponding names) and are coloured based on relationship in the corresponding dendogram.

Table 3 Eucalypt phytogeographical regions and subregions defined by analysis of Simpson's beta (β_{sim}) species turnover (letters in brackets refer to regions and subregions shown in Fig 3).

Eucalypt phytogeographical regions	Geographic subdivisions	Subregions
Monsoon (B)	Top End/Malesia	Top End/Malesia (a)
	Monsoonal Belt	East (b)
		Central (c)
		West (d)
Eremaean north (A)	West	Pilbara (a)
		Coastal (b)
	Central/eastern	Central (c)
		East (d)
Eremaean south (E)	Eastern/Central	Southern MDB (a)
		Nullarbor Plain (b)
	Western	South (d)
		North (c)
Tropical/ Subtropical (C)	Tropical	Cape York (a)
	Subtropical	QLD North (b)
		NSW South (c)
South-east (F)	Alpine	Alpine (a)
	Tasmanian/southern Victoria	Tasmania (b)
		South-eastern Victoria (c)
South-west (D)	South-eastern	South-eastern (a)
	Western	North (c)
		South (b)

DISCUSSION

Eucalypt phytogeographical regions

Our seven phytogeographical regions and 21 subregions contribute significantly to the understanding of contemporary Australian biogeography. The major split of the main two clusters suggests the existence of a north-south split of the eucalypt phytogeographical regions. The southern area might reflect historical adaptation to habitats affected by higher winter rainfall whereas the northern area might be more influenced by the summer rainfall adapting to high humidity and

extreme heat. Within the southern area, the Eremaean South and south-west share higher similarity than with the south-east. In contrast, the clusters corresponding to the monsoon
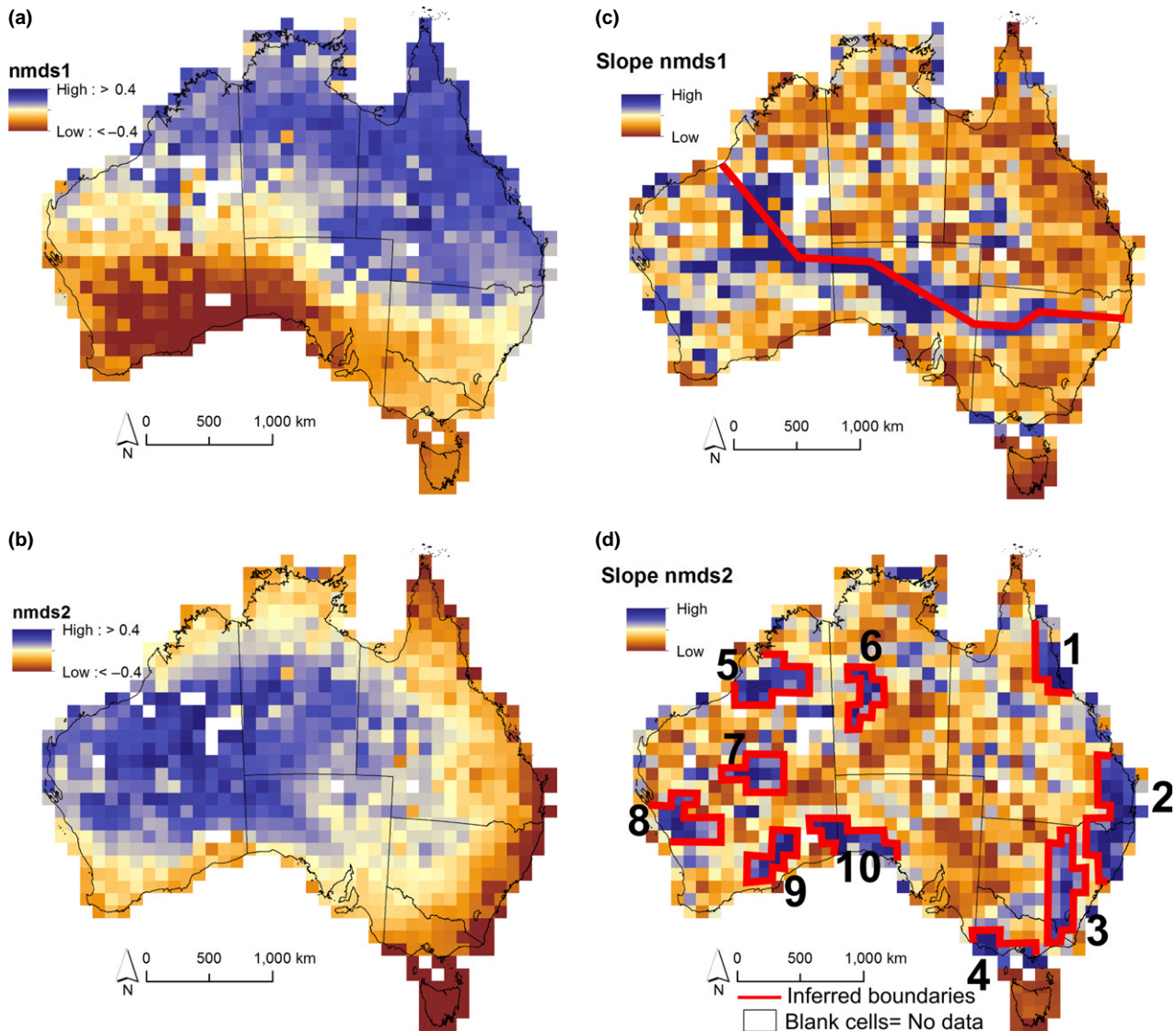
Figure 4 Species turnover of Australian eucalypts measured with the non-metric multidimensional scaling (NMDS) method for (a) axis 1 (NMDS1) and (b) axis 2 (NMDS2). The two right side panels plot the slopes of NMDS1 (c) and NMDS2 (d) and the inferred biogeographic breaks (red lines and polygons).

and Eremaean north share higher similarity than with tropical/subtropical clusters. The limits of the southern area extend east-west from Western Australia to central New South Wales. This major pattern could be explained by the effect of regolith carbonate accumulations in the soil (Hill *et al.*, 1999; McQueen *et al.*, 1999). Such a geochemical difference is a potential explanation for the presence of the major north-south split of the continent wide phytogeographical regions of the eucalypts.

Our proposed eucalypt phytogeographical regions (Fig. 2) are in broad agreement with the biomes of Australia (Burbidge, 1960; Schodde, 1989; Crisp *et al.*, 2004). The main difference between the result of our analysis and those of Burbidge (1960) is that the northern Tropical Cape York region is not differentiated as part of the monsoonal tropics biome, instead it is part of the north-eastern tropical region (Fig. 2c). The extent of Burbidge's monsoonal tropics is

larger than ours, specifically towards the central eastern region. The Eremaean zone is a single unit in Burbidge's classification while here we divide it into two distinct regions with the Eremaean north clustering with the monsoonal bioregion and not with the Eremaean south. This same relationship was also found in *Acacia* (González-Orozco *et al.*, 2013). Species endemism is a key concept to explain biogeographical patterns (Parenti & Ebach, 2009). We found that in six of the seven proposed eucalypt phytogeographical regions there is at least one centre of endemism (Table 5).

Linking eucalypt phytogeographical regions to environment

There are many examples of bioregionalizations in Australia, such as the agro-climatic classification, the environmental
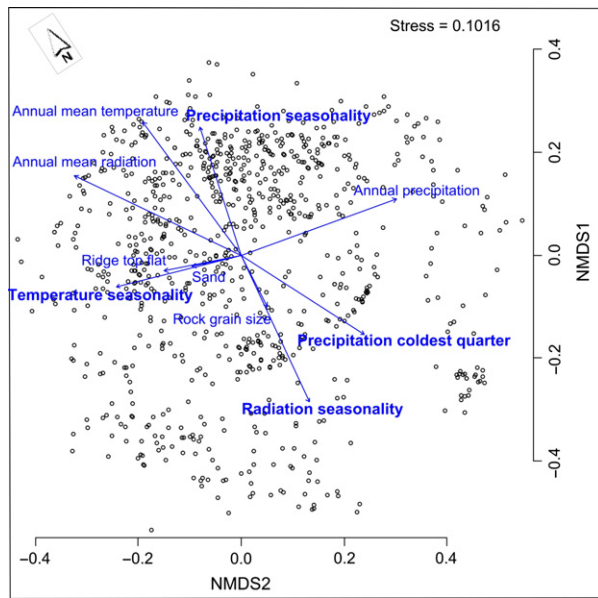
Figure 5 Non-metric multidimensional scaling (NMDS) of eleven environmental variables fitted to turnover (β_{sim}) of Australian eucalypts. Vector names representing seasonal related variables are bolded while aseasonal and non-climatic variables are not. The North arrow in the top left corner represents the geographic orientation of the NMDS values.

Table 5 Occurrence of centres of species richness and endemism per phytogeographical regions of Australian eucalypts. Numbers denote the number of centres present in each bioregion, a dash (–) denotes no centres

Eucalypt phytogeographical regions	Species Richness	Endemism
Monsoon	–	1
Eremaean north	–	2
Eremaean south	–	–
Tropical	–	1
Subtropical	1	3
South–east	1	4
South–west	1	3

during the wettest quarter of the year and rainfall patterns overall had a great effect on the species located in the northern tropical regions. Our work identified a predominant north-east and south-west geographical pattern, which fits the climatic rationale presented by Burbidge (1960). Burbidge also identified the Tropic of Capricorn as a major biome delineator: higher summer rainfall to the north and winter rainfall to the south.

The inconsistencies of environmental drivers between our study and that of Gill et al. (1985) may be due to the fact that we used more species records, a greater number of species and applied a metric that minimizes the imbalance of species richness in representing biotic turnover (see Table 6). Gill et al. also used meteorological data from the weather station nearest to each cell, whereas our climate data are derived by spatial interpolation using all surrounding stations.

Comparing eucalypt phytogeographical regions to major eucalypt communities

Our phytogeographical regions closely match with previous broad scale studies on vegetation communities in Australia that were based on expert opinion. Beadle (1981) identified four main *Eucalyptus* vegetation alliances and eight generic biogeographical regions of eucalypts. The main difference of

domain classification and the primary productivity regionalization of Australia (Hutchinson et al., 2005; Mackey et al., 2008). These are important frameworks but are strongly biophysical, as opposed to the biologically centred approach used here. The only study comparing species distribution of eucalypts to climate at the continental scale was conducted by Gill et al. (1985). They identified two eucalypt clades adapted to warm climates (*Blakella-Corymbia* and *Eudesmia*) and another two composed of mostly of species that are adapted to cool climates. The genus *Eucalyptus* contains 10 subgenera, but subgena Blakella and Corymbia comprise the subgenera *Corymbia*. Gill et al. also noted that temperature

Table 4 Gi* statistic scores for the cells comprising the six major phytogeographical regions of Australian eucalypts. Bold text signifies statistically significant (α = 0.05). N = number of grid cells per region.

	Monsoon (N = 127)	Eremaean north (N = 341)	Eremaean south (N = 204)	Tropical (N = 38)	Subtropical (N = 38)	South-east (N = 65)	South-west (N = 21)
Annual mean radiation	**6.46**	**9.83**	−2.47	−0.58	−4.18	**−15.16**	**−7.11**
Annual mean temperature	**13.75**	**7.54**	**−9.18**	**4.88**	−2.84	**−15.35**	**−6.82**
Annual mean precipitation	**10.06**	**−11.67**	**−10.53**	**11.02**	**8.80**	**8.49**	**2.21**
Percentage of clay	0.51	**2.35**	−1.64	−1.75	1.98	−0.11	**−4.28**
Precipitation coldest quarter	**−8.18**	**−7.84**	0.67	**−2.97**	**4.55**	**16.32**	**11.93**
Precipitation seasonality	**16.88**	**2.59**	**−13.73**	**8.54**	−1.73	**−10.20**	−0.83
Radiation seasonality	**−15.19**	**−6.37**	**12.91**	**−5.48**	−1.27	**13.98**	**4.71**
Ridge Top flatness	**2.56**	0.42	**4.80**	**−2.65**	**−4.82**	**−5.35**	−1.34
Rock grain size	−1.39	**−7.45**	**8.51**	−0.46	0.04	0.28	**3.63**
Percentage of sand	1.63	−0.91	−0.27	1.60	−1.80	−1.14	**2.10**
Temperature seasonality	**−12.79**	**12.39**	**6.81**	**−10.16**	−3.20	−3.96	−4.36

Table 6 Ten principal differences between the present study and that of Gill *et al.* (1985) for the analysis of the distribution of species dissimilarity and diversity of Australian eucalypts.

Study parameters	Gill *et al.* (1985)	Present study
Spatial scale	1.0 × 1.5 degrees (lat × long)	100 × 100 km grid cells
Turnover metric	Jaccard and Czeckanowski	Beta-Simpson index
Number of species	551	798
Taxonomic resolution	Species and subgenera (without *Angophora*)	*Eucalyptus*, *Angophora* and *Corymbia*
Statistical technique	PCA	NMDS
Cluster metric	UPGMA	WPGMA
Environmental variables	Ten (five temperature and five rainfall variables with no soils)	Eleven seasonal and aseasonal variables
Terminology	Zones	Bioregions and subregions
Distribution	Continental	Continental and Malesia
Diversity metric used	Species richness and absolute endemism	Species richness and relative endemism
Number of bioregions	11 major zones and 18 subgroups	Six main bioregions and 13 subregions

our study from Beadle's is that he did not define the monsoon region per se and the semi-arid and arid areas in central Australia are not split into two regions as we propose here. A more recent vegetation classification based on the National Vegetation Information System (NVIS) classification (DEWR, 2007) defined six major eucalypt vegetation groups, which broadly correspond with our phytogeographical regions.

The results of this research support previous findings regarding the location of the main centres of species richness but, interestingly, we identified new centres of endemism. The eucalypt centres of species diversity and endemism tend to be different from other groups of Australian plants and mostly occur south of the Tropic of Capricorn. For example, the biodiversity hotspot of south-west Australia is an area of high species richness and endemism for both *Acacia* (González-Orozco *et al.*, 2011) and eucalypts but not for *Glycine* (González-Orozco *et al.*, 2012*)* or bryophytes (Stevenson *et al.*, 2012). However, the species rich and endemic areas in the south-west do not overlap but are mostly adjacent to each other suggesting separate environmental niche preferences for the two lineages. *Acacia* species richness and endemism is most pronounced in a belt delimiting the south-west for the arid zone while the eucalypt species richness and endemism dominate the coastal regions. There is an area of overlap of species richness and endemism in *Acacia* and the eucalypts in the broader Stirling ranges — Fitzgerald River region of Western Australia (see area 1 in Fig. 1a). Overlapping patterns of high species richness, with fewer areas of endemism, are found in south-eastern Australia for the eucalypts, *Acacia*, hornworts liverworts and mosses (González-Orozco *et al.*, 2011, 2012; Stevenson *et al.*, 2012). This suggests that south-eastern Australia is an area of high speciation and broader geographical distributions. The Wet Tropics is an area of high species richness and endemism for all these lineages.

Bioregionalizations have been conducted on continental (Rueda *et al.*, 2010; Linder *et al.*, 2012) and global scales (Kreft & Jetz, 2010; Holt *et al.*, 2012). These works provide an alternative approach as they consider a subset of the diversity of groups such as plants, insects and vertebrates within large geographical areas whereas our study focuses on a single fully sampled lineage at a continental scale. Linder *et al.* (2012) also used β_{sim} and identified seven sub-Saharan biogeographical regions that were broadly congruent among the plant and vertebrate groups studied. However, Rueda *et al.* (2010) did not find congruence among lineage-specific bioregionalizations in Europe. An allied study on *Acacia* (González-Orozco *et al.*, 2013) revealed similar but not identical phytogeographical patterns to the eucalypts. It is possible that the differing evolutionary histories of individual lineages, when combined in a single analysis, would produce the less defined patterns that were seen by Linder *et al.* (2012) in sub-Saharan Africa. More studies are needed to better understand whether bioregionalizations of plants and animal groups are congruent (Linder *et al.*, 2012) or incongruent (Udvardy, 1975; Rueda *et al.*, 2010) and what drives the patterns.

Our finding that climate and dissimilarity of plant distributions correlate with species turnover confirms previous global studies (Buckley & Jetz, 2008). For example, Buckley and Jetz (2008) found that high levels of species turnover occur regardless of environmental turnover rates, but environmental turnover provides a lower bound for species turnover in amphibians than for birds. Because each continent has specific topographic and climatic attributes, it would not be expected to find major similarities on the main environmental control of turnover.

The patterns of eucalypt diversity identified here provide a foundation for future biogeographical studies and investigation of eucalypt environmental niches. In the eucalypts, the patterns of species richness and endemism are not tightly linked, especially in south-eastern Australia. Those taxa in the species rich areas have broad ranges, thereby lowering the corrected weighted endemism scores and suggesting multiple dispersal episodes following events of active allopatric speciation.

Limited inferences can be made on data based on species distribution without a phylogenetic context. It is probable that combining over 800 species into a single study will obscure important signals that can be determined through phylogenetics. The utilization of phylogenetic diversity (Faith 1992), phylogenetic endemism (Rosauer *et al.*, 2009) and related metrics

may better unravel the historical factors and evolutionary relationships behind the organization of biodiversity on the landscape. A thorough understanding of the basis for these patterns, including phylogeny and environmental niche preferences, can inform conservation planning decisions. Although our classification is not based on phylogenetic relationships, we found a few similarities with some phylogenetic focussed studies. Ladiges *et al.* (2011) reported that species of *Corymbia* and *Eudesmia,* analysed using area cladogram techniques, suggest differences between the monsoon tropics and the eastern areas of Australia. Here, we identified similar patterns across the larger eucalypts group. The phylogenetic structure of the eucalypts in these bioregions and at smaller scales could be driven by alternative ecological patterns, such as phylogenetic clustering or over-dispersion (Webb *et al.*, 2003).

Potential caveats

We demonstrate that bioregionalizations of a continent using species turnover of a large taxon group is a potential method to understand biogeography, as shown in other case studies (see Linder *et al.*, 2012). However, despite partitioning, the continent into meaningful biogeographical areas of species assemblages, the phytogeographical regions are not evolution-based and therefore phylogenetic approaches would benefit future studies (Ferrier *et al.*, 2007; Rosauer *et al.*, 2013).

Sampling bias is a common problem with herbarium data, and under-sampling is thus a common cause of uncertainty. We explored the potential implication of sampling bias by conducting a redundancy analysis, calculated as the ratio of species records to number of samples per grid cell (Garcillán *et al.*, 2003). We found that only 274 of all 906 grid cells analysed had redundancies less than 30% (see grid cells in green and blue shades; Appendix S1). This indicates that 70% of the continent is comparatively well sampled. The poorly sampled areas, which are often remote, tend to correspond with areas of low turnover values.

The grid cell size may also have an effect on the turnover patterns (Barton *et al.*, 2013). A pilot test (results not shown) that assessed the effect of grid cell size (50 km × 50 km; 25 km × 25 km) on the mapping of the phytogeographical regions found no major spatial difference in terms of number of phytogeographical regions generated. However, we observed that the resolution has a small effect on the boundaries of the bioregions.

CONCLUSION

Rainfall plays a key role for northern Australian eucalypt assemblages, whereas temperature and solar radiation are more important in the south and south-eastern regions, specifically south of the Tropic of Capricorn. Current climate projections suggest warmer temperatures for eucalypts in Australia, particularly the southern populations (Hughes *et al.*, 1996). Temperature is a key driver of eucalypt species turnover, which highlights the importance of special care

when managing biodiversity around areas located in southern latitudes. Species turnover patterns of eucalypts in the western part of the continent correlate more with non-climatic factors such as topographic and soil properties. Although the proposed phytogeographical regions are exclusive to eucalypts, our method can be applied to any geographical scale providing sufficient data with the appropriate taxonomic and spatial detail are available.

REFERENCES

ALWRA, National Land & Water Resources Audit. (2002) *Australian terrestrial biodiversity assessment.* Chapter 7: Acacias and Eucalypts. pp. 101–112. Commonwealth Australia, Canberra, Australia.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, A. (1994) Determining species responses to an environmental gradient by means of a β-function. *Journal of Vegetation Science*, **5**, 215–228.

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Didham, R.K. (2013) The spatial scaling of beta diversity. *Global Ecology and Biogeography*, **22**, 639–647.

Beadle, N.C.W. (1981) *The vegetation of Australia.* pp. 690. Cambridge University Press, Cambridge.

Brooker, M.I.H. (2000) A new classification of the genus *Eucalyptus* L'Hér. (Myrtaceae). *Australian Systematic Botany*, **13**, 79–148.

Brooker, M.I.H. & Kleining, D.A. (1983) *Field guide to Eucalypts. South-eastern Australia*, 3rd edn, Vol. 1. Bloomings Books, Melbourne, Vic., Australia.

Brooker, M.I.H., Slee, A.V., Connors, J.R. & Duffy, S.M. (2006) *EUCLID Eucalypts of southern Australia*, 3rd edn. CD; CSIRO Publishing, Collingwood, Australia.

Buckley, L.B. & Jetz, W. (2008) Linking global turnover of species and environments. *PNAS*, **105**, 17836–17841.

Burbidge, N.T. (1960) The phytogeography of the Australian regions. *Australian Journal of Botany*, **8**, 387–392.

Council of Heads of Australasian Herbaria –CHAH. (2010). Australian Plant Census. Available at: http://www.anbg.gov.au/chah/apc/index.html (accessed 27 August 2013).

Crisp, M.D., Laffan, S., Linder, H.P. & Munro, A. (2001) Endemism in the Australian Flora. *Journal of Biogeography*, **28**, 183–198.

Crisp, M.D., Cook, L. & Steane, D. (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 1551–1571.

DEWR. (2007) *Australia's native vegetation: a summary of Australia's major vegetation groups, 2007*. NVI_3. Australian Government, Canberra. http://www.environment.gov.au/erin/nvis/

Dorothy, A.S., Nicolle, D., McKinnon, G.E., Vaillancourt, R.E. & Potts, B.M. (2002) Higher-level relationships among the eucalypts are resolved by ITS-sequence data. *Australian Systematic Botany*, **15**, 49–62.

Ebach, M.C. (2012) A history of biogeographical regionalisation in Australia. *Zootaxa*, **3392**, 1–9.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13**, 252–264.

Gallant, J. & Dowling, T. (2003) A multi-resolution index of valley bottom flatness for mapping depositional areas. *Water Resources Research*, **39**, 1347.

Garcillán, P.P., Ezcurra, E. & Riemann, H. (2003) Distribution and species richness of woody dry land legumes in Baja California, Mexico. *Journal of Vegetation Science*, **14**, 475–486.

Gill, A.M., Belbin, L. & Chippendale, G.M. (1985) *Phytogeography of* Eucalyptus *in Australia*. Australian Flora and Fauna series, No 3. pp. 53. Australian Government Publishing Service, Canberra, Australia.

González-Orozco, C.E., Laffan, S.W. & Miller, J.T. (2011) Spatial distribution of species richness and endemism of the genus *Acacia* in Australia. *Australian Journal of Botany*, **59**, 600–608.

González-Orozco, C.E., Brown, A.H.D., Knerr, N., Miller, J.T. & Doyle, J.J. (2012) Hotspots of diversity of wild Australian soybean relatives and their conservation *in situ*. *Conservation Genetics*, **13**, 1269–1281.

González-Orozco, C.E., Laffan, S.W., Knerr, N. & Miller, J.T. (2013) A biogeographical regionalisation of Australian *Acacia* species. *Journal of Biogeography*. http://onlinelibrary.wiley.com/doi/10.1111/jbi.12153/pdf

Hill, K.D. & Johnson, L.A.S. (1995) Systematic studies in the eucalypts 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). *Telopea*, **6**, 185–504.

Hill, S.M., McQueen, K.G. & Foster, K.A. (1999) *Regolith carbonate accumulations in western and central NSW: characteristics and potential as an exploration sampling medium*. New Approaches to an Old Continent. Cooperative Research Centre for Landscape Evolution and Mineral Exploration. pp. 191–208. Perth, Australia.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jonsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbeck, C. (2012) An update of Wallace's Zoogeographic regions of the world. *Science*, **339**, 74–78.

Houlder, D.J. (2000) *ANUCLIM user's guide*. Version 5.1. Centre for Resource and Environmental Studies, Australian national University, Canberra. http://fennerschool.anu.edu.au/publications/software/anuclim.php

Hughes, L., Cawsey, E.M. & Westoby, M. (1996) Climatic range sizes of *Eucalypts* species in relation to future climate change. *Global Ecology and Biogeography Letters*, **5**, 23–29.

Hutchinson, M.F., Houlder, D.J., Nix, H.A. & McMahon, J.P. (2000) *ANUCLIM users guide version 5.1*. Centre for Resource and Environmental Studies, Australian National University, Canberra.

Hutchinson, M.F., McIntyre, S., Hobbs, R.J., Stein, J.L., Garnett, S. & Kinloch, J. (2005) Integrating a global agroclimatic classification with bioregional boundaries in Australia. *Global Ecology and Biogeography*, **14**, 197–212.

Johnston, R.M., Barry, S.J., Bleys, E., Bui, E.N., Moran, C.J., Simon, D.A.P., Carlile, P., McKenzie, N.J., Henderson, B.L., Chapman, G., Imhoff, M., Maschmedt, D., Howe, D., Grose, C., Schoknecht, N., Powell, B. & Grundy, M. (2003) ASRIS: the database. *Australian Journal of Soil Research*, **41**, 1021–1036.

Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographic regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.

Külheim, C., Yeoh, S.H., Wallis, I.R., Laffan, S.W., Moran, G.F. & Foley, W.J. (2011) The molecular basis of quantitative variation in foliar secondary metabolites in *Eucalyptus globulus*. *New Phytologist*, **191**, 1041–1053.

Ladiges, P.Y. (1997) Phylogenetic history and classification of eucalypts. *Eucalypt ecology: individuals to ecosystems*. (ed. by J. E Williams and J.C. Z Woinarski), pp. 16–29. Cambridge University Press, Cambridge.

Ladiges, P.Y., Udovicic, F. & Drinnan, A.N. (1995) Eucalypt phylogeny—molecules and morphology. *Australian Systematic Botany*, **8**, 483–497.

Ladiges, P.Y., Udovicic, F. & Nelson, G. (2003) Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. *Journal of Biogeography*, **30**, 989–998.

Ladiges, P.Y., Parra-O, C., Gibbs, A., Udovicic, F., Nelson, G. & Bayly, M. (2011) Historical biogeographical patterns in continental Australia: congruence among areas of endemism of two major clades of eucalypts. *Cladistics*, **27**, 29–41.

Laffan, S.W. (2002) Using process models to improve spatial analysis. *International Journal of Geographical Information Science*, **16**, 245–257.

Laffan, S.W. & Crisp, M.D. (2003) Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *Journal of Biogeography*, **30**, 511–520.

Laffan, S.W., Lubarsky, E. & Rosauer, D.F. (2010) Biodiverse, a tool for the spatial analysis of biological and related diversity. *Ecography*, **33**, 643–647.

Laffan, S.W., Ramp, D. & Roger, E. (2013) Assessing reserve representation using endemism – the family Myrtaceae in the Greater Blue Mountains World Heritage Area. *Journal of Biogeography*, **40**, 570–578.

Lepschi, B. & Monro, A. (2011) Australian plant census: November 2011 update. *Journal of the Australian Network for Plant Conservation*, **20**, 25–26.

Linder, H.P., de Klerk, H.M., Born, J., Burgess, N.D., Fjeldså, J. & Rahbek, C. (2012) The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, **39**, 1189–1205.

Mackey, B.G., Berry, S.L. & Brown, T. (2008) Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent. *Journal of Biogeography*, **35**, 213–229.

McQueen, K.G., Hill, S.M. & Foster, K.A. (1999) The nature and distribution of regolight carbonate accumulations in southeastern Australia and their potential as a sampling medium in geochemical exploration. *Journal of Geochemical Exploration*, **67**, 67–82.

Morrone, J.J. & Crisci, J.V. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics*, **26**, 373–401.

Nicolle, D. (1997). *Eucalypts of South Australia*. D Nicolle, Adelaide.

Nicolle, D. (2006). *Eucalypts of Victoria and Tasmania*. Bloomings Books, Melbourne, Vic., Australia.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Peter Solymos, M., Stevens, H.H. & Wagner, H. (2012) Package 'vegan', version 2.0-5.

Orme, C.D., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Parenti, L.R. & Ebach, M. (2009) Building blocks of biogeography. *Comparative biogeography: discovering and classifying biogeographical patterns of a dynamic earth*. pp. 53–74. University of California Press, Berkeley.

R Development Core Team. (2005) *R: a language and environment for statistical computing*. R foundation for Statistical Computing, Vienna. Available at: http://cran.r-project.org/.

Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, **18**, 4061–4072.

Rosauer, D., Ferrier, S., Williams, K.J., Manion, G., Keogh, J.S. & Laffan, S.W. (2013) Phylogenetic generalised dissimilarity modelling: a new approach to analysing and predicting spatial turnover in the phylogenetic composition of communities. *Ecography*, doi: 10.1111/j.16000587.2013.00466.x.

Rueda, M., Rodríguez, M.A. & Hawkins, B.A. (2010) Towards a biogeographic regionalization of the European biota. *Journal of Biogeography*, **37**, 2067–2076.

Schodde, R. (1989) Nancy Burbidge memorial lecture. *Australian Systematic Botany Society Newsletter*, **60**, 2–11.

Stevenson, L.A., González-Orozco, C.E., Knerr, N., Cargill, D.C. & Miller, J.M. (2012) Species richness and endemism of Australian bryophytes. *Journal of Bryology*, **34**, 101–107.

Thackway, R. & Cresswell, I.D. (1995) *An interim biogeographic regionalisation for Australia: a framework for establishing the National System of Reserves, Version 4.0.* pp. 36. Australian nature Conservation Agency, Canberra.

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

Udvardy, M.D.F. (1975) *A classification of the biogeographical provinces of the world*. IUCN Occasional Paper (No 18). pp. 49. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Wallace, A.R. (1894) What are zoological regions? *Nature*, **49**, 610–613.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2003) Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Sampling redundancy map.

Appendix S2 Statistical (mean, 5th percentile, 95th percentile) maps of the most significant environmental variables.

Appendix S3 Gi* statistic results for the floristic subregions of Australian eucalypts defined by 11 environmental variables. Black bolded means statistically significant ($\alpha = 0.05$). N = number of grid cells per subregion.

Appendix S4 Turnover map and dendrogram of the 50 km × 50 km grid cells analyses. Results of the 25 km × 25 km are not shown.

Appendix S5 Eucalypt point records for Australia and Malesia.

BIOSKETCH

Carlos E. González-Orozco is a postdoctoral fellow at the Centre for Australian National Biodiversity Research, CSIRO Plant Industry. His research interests are biogeography and phylogeography with particular focus on: (1) spatial analysis of biodiversity and their relationship with the environment, (2) spatial analysis of phylogenetic diversity/endemism, (3) development of new generation of bioregionalizations. To reveal the patterns and understand the processes that originate diversity, endemism and evolutionary history of organism is one of the main objectives.

Author's contributions: C.G. (lead writing, ideas, spatial analyses), A.T. (ideas, writing, compilation of dataset), N.K. (compilation of dataset), S.L. (spatial analyses, writing, ideas), J.M. (ideas, writing).

Editor: David Richardson