

Phylogenetic approaches reveal biodiversity threats under climate change

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Predicting the consequences of climate change for biodiversity is critical to conservation efforts^{1–3}. Extensive range losses have been predicted for thousands of individual species⁴, but less is known about how climate change might impact whole clades¹ and landscape-scale patterns of biodiversity⁵. Here, we show that climate change scenarios imply significant changes in phylogenetic diversity and phylogenetic endemism at a continental scale in Australia using the hyper-diverse clade of eucalypts. We predict that within the next 60 years the vast majority of species distributions (91%) across Australia will shrink in size (on average by 51%) and shift south on the basis of projected suitable climatic space. Geographic areas currently with high phylogenetic diversity and endemism are predicted to change substantially in future climate scenarios. Approximately 90% of the current areas with concentrations of palaeo-endemism⁶ (that is, places with old evolutionary diversity) are predicted to disappear or shift their location. These findings show that climate change threatens whole clades of the phylogenetic tree, and that the outlined approach can be used to forecast areas of biodiversity losses and continental-scale impacts of climate change.

By combining species distribution models (SDMs) with measures of evolutionary diversity, we can predict how climate change might impact the tree of life in the future^{1,7,8}. Preserving the tree of life is increasingly recognized as an important consideration for conservation in Australia; globally, this evolutionary heritage provides a storehouse of unanticipated benefits for future generations, and locally it helps ensure resilient ecosystems and ongoing delivery of their services^{9–12}. The most commonly used metric to quantify the diversity represented by the tree of life is phylogenetic diversity (PD), which represents the shared evolutionary history of species present in a region and is measured as the sum of branch lengths in the phylogenetic tree linking the species present¹⁰. PD does not include information on rarity of

lineages, which is another important concern for conservation priorities. Phylogenetic endemism (PE) addresses this problem by incorporating the degree of spatial restriction of phylogenetic branches found in an area, relative to all other areas¹³. This useful property means that PE can be used to identify areas that host relatively unique diversity, such as range-restricted 'long-branch' lineages (that is, palaeo-endemics—species or clades with no living close relatives such as the reptile Tuatara, *Sphenodon*, or the fish Coelacanth, *Latimeria*).

In addition to preserving past evolutionary heritage, protecting areas that hold rapidly diversifying, range-restricted lineages (that is, neo-endemics) is a priority, because those lineages hold the key to future evolutionary potential. Previous studies have considered how climate change will impact the evolutionary heritage represented by PD^{1,7,8}. PD is expected to be correlated with species richness. Therefore, we applied a spatial randomization to evaluate departures of PD and PE from expectations⁶. Consequently, our PD-based metrics are decoupled from their corresponding species-based metrics. Here we present the first analysis describing how both the past and future of evolution might be impacted by climate change using model predictions and newly developed phylogenetic metrics that take into account relative branch lengths.

We explored our approach for a key taxonomic group, Australian eucalypts (genera *Eucalyptus*, *Corymbia* and *Angophora*). Australian eucalypts are an appropriate biological model because they are a hyper-diverse group (>800 species) that dominate forest canopies and ecosystems across much of the continent. Eucalypts are mostly endemic to Australia and have a broad biogeographical diversity¹⁴. They are of global interest due to their widespread use in forestry¹⁵. They form a monophyletic lineage within the Myrtaceae family^{16–19}, including the few eucalypt species that occur outside Australia. Here we examine the expected shift in the geographic ranges of 657 species of eucalypt across Australia, comparing present ranges with those under forecast climate change scenarios for the years

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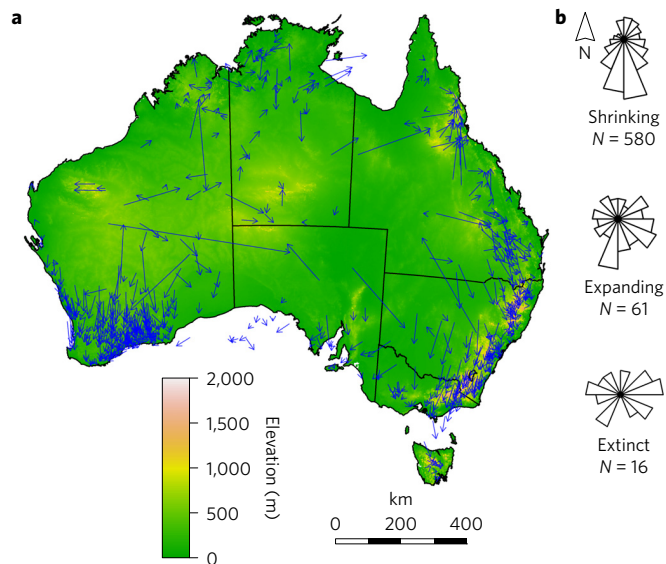


Figure 1 | Variation in the predicted distribution of the suitable climate space of 657 Australian eucalypt species from 2014 to 2085. **a**, Shift in the predicted species distribution where arrows present the magnitude and direction of change in distribution at the centroid of the climatic space. **b**, Plots showing the general direction of the distributional change for species that have shrinking distributions, expanding distributions or go extinct at the last time point.

2025, 2045, 2065 and 2085. We used SDMs to predict changes in geographic ranges and the direction in which ranges are likely to shift under future climate scenarios. SDMs have limitations when predicting responses to climate change in species²⁰ (for example, climatic adaptability) and communities (for example, species interactions). We accounted for some of the well-known weaknesses of SDMs by explicitly considering spatial bias and over-fitting, and comparing models with and without dispersal. The dispersal and non-dispersal scenarios produced very similar patterns, so we report only the results from the dispersal scenario.

Our study's novel findings regarding effects of climate change on phylogenetic diversity are grounded in our descriptions of impacts at the species level that corroborate previous findings. Eucalypt species are known to be threatened by climate change in Australia with previous results suggesting 53% of all *Eucalyptus* species predicted to be outside their current climate conditions by 2070 under a 3 °C warming scenario²¹. More recent SDM modelling for eucalypts suggests species ranges across the continent will contract and shift in both lateral and poleward directions, and the central desert areas will be particularly affected²². Our models predicted that by 2085, the current geographic range of 91% of the 657 eucalypt species will shrink by an average of 51%, with 2.4% of species predicted to become extinct because their climate space will disappear entirely. Relatively few species (9%) are predicted to expand their geographic range (Fig. 1; see also Supplementary Information 2 for range size, percentage change, type of shift, shift magnitude and shift direction; and Supplementary Information 4 for maps for each of the 657 species).

To understand how these losses in species will manifest as changes in evolutionary diversity across the landscape, we calculated present and future PD¹⁰ and PE¹³ for all grid cells (~25 km × 25 km). These analyses predict that on average 2% of PD (decline in PD grid cells) will be lost across Australia by 2085 (Supplementary Fig. 1). Losses will occur in places recognized as national¹⁴ and global biodiversity hotspots²³. Additionally, we found that the rate of turnover of PD increases over time, with a higher proportion of major changes occurring in southern Australia

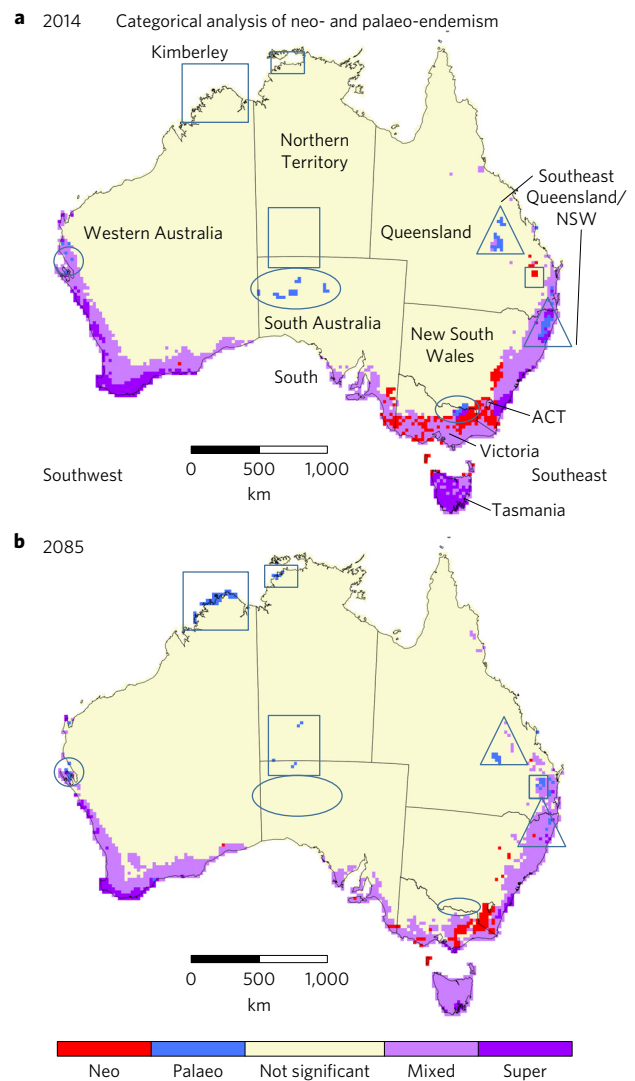


Figure 2 | Areas of phylogenetic endemism using categorical analysis of neo- and palaeo-endemism (CANAPE) for 657 species of eucalypts in Australia for projected climate change scenarios at 2014 and 2085. **a, b**, CANAPE map for 2014 (**a**) and 2085 (**b**). Ellipses indicate places where current areas of palaeo-endemism disappear; rectangles indicate places where new areas of palaeo-endemism appear; triangles indicate where current areas of palaeo- or neo-endemism weaken. Beige areas do not depart significantly from random expectation.

(Supplementary Fig. 9). Specifically, Mediterranean, temperate and grassland ecosystems will face the greatest proportional change in clades present over time. This trend is accompanied by an increasing homogenization over the landscape. The average rate of phylogenetic turnover between all pairs of cells within a given year will decrease from 0.58 in the present to 0.50 in 2085 (Supplementary Table 1), suggesting an increase in average spatial homogeneity of phylogenetic composition (or phylogenetic homogenization) in the future. This spatial homogenization of PD has been documented previously for diverse groups in Europe¹, and is suggested by past and current climate-driven plant extinctions for Thoreau's woods in the US and some temperate tree floras in Europe^{24,25}. Here, for the first time, we show the potential effects of climate change leading to PD loss in the future for a significant biological group of the Southern Hemisphere.

In contrast, PE is predicted to increase spatially in some of the areas of key diversity hotspots. In general, species endemism and PE are measures of rarity, and therefore, endemism tends to increase

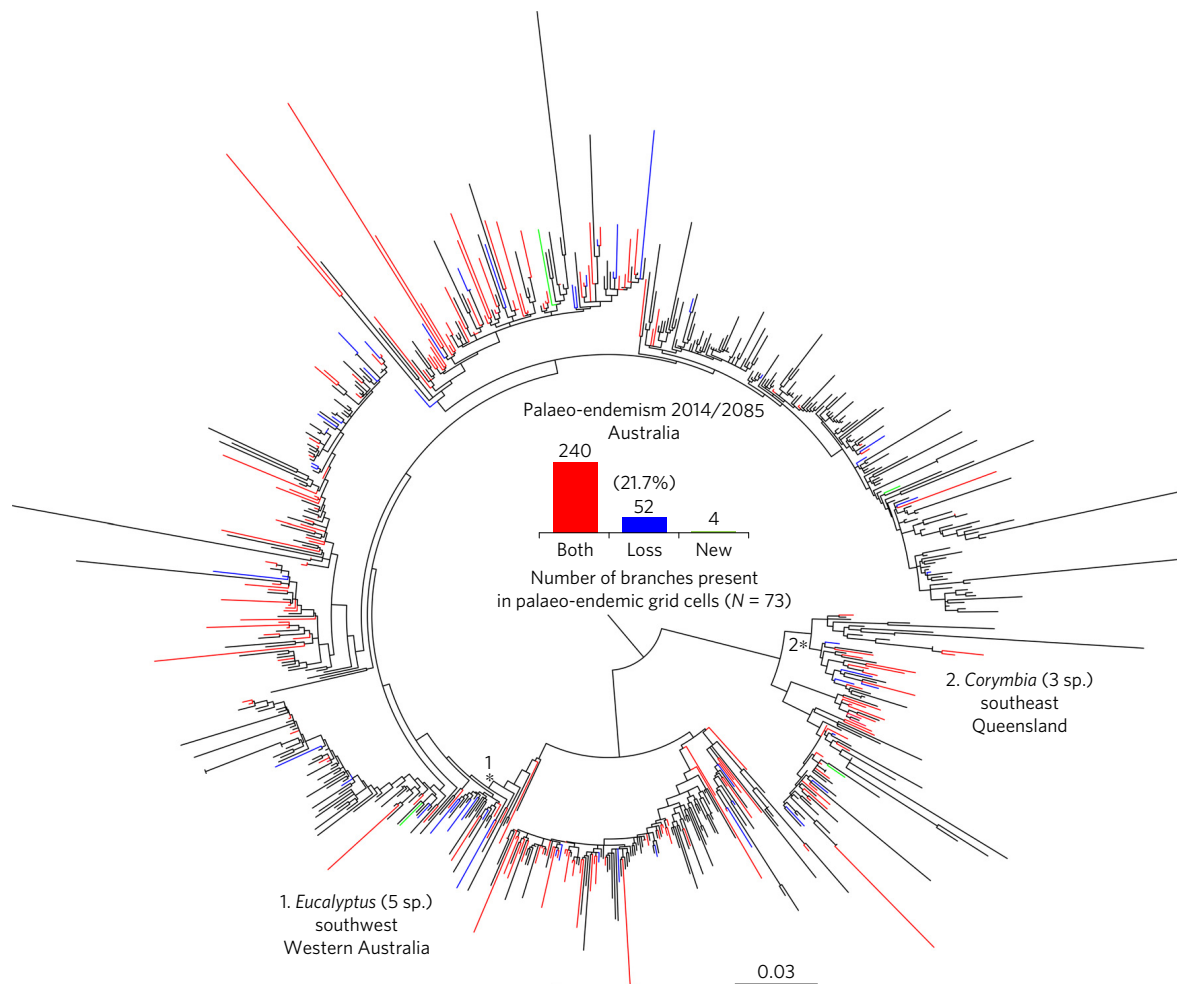


Figure 3 | Effects of projected climate change scenarios, between 2014 and 2085, on species of eucalypts found in current areas of palaeo-endemism across Australia. Highlighted branches in the phylogenetic tree are present in the 73 grid cells that had significant palaeo-endemism in Australia in 2014 (blue grid cells in ellipses Fig. 2a). Branches predicted to be lost from the 73 grid cells by 2085 are shown in blue, branches predicted to immigrate by 2085 are shown in green, and branches common to both periods are shown in red. Clades marked with an asterisk refer to places in the phylogeny corresponding to palaeo-endemism where individual branches were removed from the phylogeny consistently over time.

in the areas that hold the remaining portions of species ranges. The increase in PE is a result of lineages becoming more range-restricted. For example, in southwestern Western Australia, an internationally recognized biodiversity hotspot, species are predicted to retract toward the coast, causing some coastal cells to have high PE in the future (Supplementary Fig. 1e). Predicting the location of high-PE areas in the future is important from a conservation standpoint because these locations are likely to be the sites of concentrations of rare elements of diversity in the future, and, therefore, will be strategic areas for preventing further PD losses.

Two derived metrics, relative phylogenetic diversity (RPD) and relative phylogenetic endemism (RPE)⁶, can be used to better understand anticipated impacts on unusually long or short branches. These metrics reveal information about the underlying evolutionary processes that we seek to understand and conserve⁶ and also because they point to areas that encompass old and highly unique lineages that, once lost, will significantly reduce the breadth of biodiversity. Sites with many very long branches are important repositories of unique evolutionary history and trait diversity²⁶; sites with many short branches might indicate places with the potential for generating evolutionary adaptation and speciation in the future.

The RPD and RPE metrics reveal these patterns through an assessment that asks whether the contribution of unusually long or short branches to PD or PE in a grid cell is greater or less

than expected by chance. RPD (or RPE) is the ratio of PD (or PE) measured using the set of species in that grid cell on the observed tree of the 657 eucalypt species to that measured on a comparison tree with the same topology but with all branches adjusted to be of equal (average) length⁶, with significant large or small ratios determined by a spatial randomization test (see Methods for details of randomization test)²⁷. We find both areas of significantly high and significantly low RPD are predicted to decline in size (~10%) by 2085 (Supplementary Fig. 2), indicating that unusually long- and short-branch lineages will disappear within sites.

Endemism can result either from younger lineages that have yet to expand their range or from older lineages that are relicts of a previously broader distribution. RPE allows the identification of centres of palaeo-endemism (range-restricted long branches), centres of neo-endemism (range-restricted short branches), or both (centres of mixed endemism, termed 'super-endemism'), through a recently developed method called CANAPE (categorical analysis of neo- and palaeo-endemism; see Methods)⁶. We find that the current areas of palaeo-, neo- and super-endemism are predicted to significantly shrink (~50%) in size by 2085 (Fig. 2 and Supplementary Fig. 3a–e). This suggests that current areas of significant phylogenetic endemism may decline as lineages either go extinct or move to different locations (Figs 2 and 3) with climate change.

Areas of palaeo-endemism are particularly impacted; $\geq 90\%$ of the current areas with significantly high palaeo-endemism will disappear or shift to new places by 2085 (Fig. 2 ellipses). Most of the large loss of palaeo-endemism is due to shrinking geographic range of lineages (Supplementary Fig. 4). This large loss of palaeo-endemism is a loss in the number of grid cells falling into that category. Shrinking ranges can increase the palaeo-endemism of a cell that retains those long branches, but overall decreases of palaeo-endemism areas reflect the loss of those branches from areas. For example, between the present and 2085, 64.6% of species' geographic ranges within current palaeo-endemism areas will shrink (Supplementary Fig. 4), thus impacting their contribution to overall PE of these areas. There are currently 73 grid cells with significant eucalypt palaeo-endemism in Australia, containing 240 species. By 2085, 52 of these species are predicted to go extinct or migrate elsewhere (Fig. 3). Consequently, most of these grid cells will cease to be areas of palaeo-endemism by 2085. Declines of palaeo-endemism areas tended to be even larger in the no-dispersal scenario, which otherwise gave similar results to the dispersal scenario reported in the text (Supplementary Fig. 3f–j). These results show that areas of palaeo-endemism are not necessarily places of long-term stability, but instead may be highly threatened and mobile.

We also found that, in a few cases, new areas of palaeo-endemism (Fig. 2, squares) are predicted to form. The main reason that palaeo-endemism sites appear is because current widespread long-branch lineages become more range-restricted under climate change. These predicted new centres of palaeo-endemism will be important for future conservation because they represent predicted areas that have the potential to harbour rare long branches.

Lineages are also predicted to disappear from places where new concentrations of palaeo-endemism will form (see the square in central Australia and the larger rectangle in the far top left in Fig. 2b). These sites currently contain 70 and 57 species and we predict that 23.3% and 7% of those species, respectively, will be locally extinct by 2085 (Fig. 2 and Supplementary Fig. 5c,d).

Overall, the extinction of whole lineages is likely to occur as a result of severe reductions of climatic space (Supplementary Fig. 5a–d; and species list in Supplementary Information 1 and Tables 1–4). The effect on the phylogeny was not evenly distributed as has been previously reported in some cases²⁴, and we identified potential extinction of five species of *Eucalyptus* in Southwest Australia and three of *Corymbia* in southeast Queensland. This could be considered as an early sign of phylogenetic extirpation²⁵ or extinction of lineages of eucalypts (Fig. 3).

Few studies have addressed the impact of climate change on PD²⁸ and ours is the first to take the additional step of showing how climate change might affect PE including centres of palaeo-(old) and neo-(young) endemism across a continental-scale landscape. Our approach can be considered as an early warning system for forecasting biodiversity loss across the landscape, critically expressed as loss of evolutionary heritage and evolutionary potential. Here we show that the contraction of lineage ranges expected with climate change is likely to reduce diversity at most locations, homogenize the landscape, and particularly impact rare long- and short-branch lineages, which might cause significant losses to the tree of life and reduce genetic adaptive potential of eucalypts under climate change^{29,30}. Faced with substantial losses to biodiversity with climate change, our approach allows the identification of areas that are key to preventing further biodiversity loss.

Specifically, we found major shifts in eucalypts' modelled distributions which, if realized, would lead to a shrinkage of current areas of high phylogenetic endemism for the species group along all the southwest, southeast and southern coastal regions of Australia. We find that Tasmania, due to its lower latitude and more temperate

climate, might become a very important refugium, while Victoria is more prone to losing areas of neo-endemism. Current hotspots of palaeo-endemism in southeast Queensland, northern coastal New South Wales and central Australia are also predicted to be impacted severely. Conversely, new concentrations of palaeo-endemism are predicted to occur in the Kimberley and northern coastal region demonstrating the potential of our methods to identify key areas that might be important refugia in the future.

Methods

Methods and any associated references are available in the [online version of the paper](#).

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Author contributions

All authors contributed to project conception. C.E.G.-O., L.J.P., A.H.T., N.K., B.G. and S.W.L. conducted analyses. A.H.T., M.D., C.K. and J.T.M. developed the phylogeny. A.H.T., N.K., C.E.G.-O., L.J.P. and N.B. compiled and corrected species spatial data records. C.E.G.-O. wrote the manuscript draft and all authors contributed to interpretation of the results and writing of the final paper.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints.

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Competing financial interests

The authors declare no competing financial interests.

Methods

Spatial data and species distribution modelling. We modelled present and future distributions of current and four future time points (2025, 2045, 2065 and 2085) for all 766 eucalypt species (~163,000 occurrence records) found in Australia (only 16 are endemic to another country) at a 5-km pixel resolution using a dispersal and a no-dispersal scenario. Data (presence-only) were extracted from Australia's Virtual Herbarium database (AVH) accessed in October 2011 (<http://avh.chah.org.au>). Species names were rectified using the current species list found in Euclid Version 3.0 (ref. 31) and experts were consulted in particular cases when naming history was difficult to reconstruct. Latitudinal biases were corrected by spatial geo-rectifications. Points outside the known natural range were removed for each species on the basis of range maps and expert opinion, and pre-1950 records were removed to limit spatial uncertainty³².

We used the Representative Concentration Pathway 6.0 scenario for the Hadley global climate model (hadcm3, <http://wallaceinitiative.org>). We focused on this moderate climate scenario because of its fit with the Australian strategy on emission reductions, and because the literature suggests that eucalypts will be significantly affected under a 3 °C warming by 2070²¹. Strictly, our predictions are therefore valid only for this scenario, but as it is an intermediate scenario our predicted responses are most likely also of the intermediate type. In case there is a reason in the future to suggest a different scenario to be more likely our approach can be easily adapted to such a scenario. We used a simplified set of predictor variables that we believe to be physiologically relevant (maximum temperature and dry season rainfall) with strong predictive power²², spatial variables (latitude and longitude) and one edaphic variable (median percentage of clay content derived from the 1:2 M Atlas of Australian Soils^{33,34}). Spatial predictors were included in the models because they help constrain the modelled distributions to a more realistic spatial extent based on an initial trial of 20 species with good distribution data.

The AVH data set is heavily influenced by road-based sampling, which was accounted for by including distance to roads as a predictor in each model, then setting distance to roads to zero for prediction (for present and future scenarios). Models were fitted using MaxEnt³⁵ in the R package 'dismo' with a random background sample of 20,000 records (the same sample for each species), randomly distributed across Australia and uniform for all species. We used only 'hinge features' because they tend to increase model performance without increasing model complexity³⁶. Hinge features provide smoother response curves, which may more closely approximate the species' fundamental niche³⁷. Model fit was evaluated with area under the ROC (receiver operating characteristic) curve from a fivefold cross-validation for each species (see values for area under the curve in Supplementary Information 3). A Maxent logistic threshold (maximum training sensitivity plus specificity) for each species was applied to convert habitat suitability into presences and absences for present and future scenarios.

In the no-dispersal scenario, we used the same set of modelling parameters described above, but prevented colonization. The present distributions are identical in the dispersal and no-dispersal scenario. In each subsequent time period, species are not allowed to disperse to cells not occupied in the previous time step.

Molecular data. DNA data for the study were gathered by using existing and newly generated nuclear (ITS and ETS) and chloroplast sequences (*matK* and *psbA-trnH*) that were successfully amplified for 711 eucalypt species (see Supplementary Information 5, Table for GenBank accessions). Leaves for DNA extraction were sourced from numerous field trips, botanical gardens, arboreta and herbaria from multiple locations around Australia. In total, 2,560 gene sequences were used in the study; 237 were mined from GenBank, and 2,323 were newly generated for this project. These sequences represented the 711 eucalypt species and 21 taxa from other Myrtaceae tribes that were used to root the phylogeny (Supplementary Fig. 6). Individual locus alignments were constructed using Muscle³⁸ and adjusted manually in Se-AL (ref. 39).

The phylogenetic analysis was performed on the concatenated alignment using maximum likelihood in the CIPRES Portal (www.phylo.org), utilizing the RAXML HPC BlackBox tool with a partition model set for each locus, with bootstrapping set to automatically halt, which occurred after 550 replicates. The ML tree with bootstrap values is shown in Supplementary Fig. 7. Supplementary Fig. 8 is a bi-plot of branch length versus bootstrap score, and shows that low bootstrap scores were restricted to very short branches. The uncertainty in these short branches did not affect the analyses presented here, since the better supported long branches contribute most of the PD.

Species range shift analyses. The mean centre of distributional area using the Maxent habitat suitability maps under present and future scenarios was estimated for the 657 species with matching phylogenetic data and SDMs following established methods⁴⁰. This analysis showed the magnitude and direction of change of the mean centre of the climate space for each species between the present and 2085. Species were grouped according to their distribution change from the present, namely into 'expanding' or 'shrinking' if the predicted suitable climate space of a species increased or decreased between the present and 2085, respectively. Species whose suitable climate space was predicted to become extinct

by 2085 were classified as 'extinct'. The 'dispersal' scenario assumes all species can disperse across the landscape. However, the use of spatial variables in the models indirectly accounts for some dispersal limitation, effectively limiting the potential of species to disperse to distant sites. We believe this spatial dispersal limitation is realistic given the biology of eucalypts, with most species having relatively heavy seeds without specialized dispersal mechanisms that simply drop to the ground when shed. Given the tree height, seed weights, and average wind speeds, most eucalypt species would not be expected to disperse beyond a single grid cell during the time period in this study without a rare long-distance dispersal event⁴¹.

Spatial phylogenetic analyses of modelled distributions. The SDM suitability values were aggregated at ~25 km × 25 km to a total of 12,813 grid cells and used to calculate species richness (SR), weighted endemism (WE), phylogenetic diversity (PD)¹⁰, phylogenetic endemism (PE)¹³, relative phylogenetic diversity (RPD) and relative phylogenetic endemism (RPE) in the Biodiverse software⁴² for 657 species. SR and WE results reported in Supplementary Fig. 1 were calculated on the basis of all 766 species because they did not require a phylogenetic tree. All phylogenetic metrics were calculated on the basis of the 657 species that are in the phylogeny. A spatial randomization based on 999 trials was applied to these metrics⁶. The purpose of the randomization is to identify whether the observed values were significantly different from a random selection of the same number of terminal taxa from the tree.

RPE is applied in a two-step test called categorical analysis of neo- and palaeo-endemism (CANAPE) using the same spatial randomization⁶. The first step of CANAPE determines whether a location is a centre of high phylogenetic endemism by applying a one-tailed test (for large values) to both the numerator and denominator of RPE (that is, PE measured on the observed tree in the numerator and PE measured on a comparison tree where all branches are of equal (average) length in the denominator). Then, for grid cells passing this test, the second step applies a two-tailed test to the RPE ratio to identify cells dominated by unusually short range-restricted branches (centres of neo-endemism), unusually long range-restricted branches (centres of palaeo-endemism), or both (centres of mixed endemism, termed 'super-endemism' if both the numerator and denominator of RPE are highly significant)⁶.

Phylogenetic turnover analyses of modelled distributions. Two spatial turnover analyses using the Phylo Sørensen index⁴³ were conducted in Biodiverse⁴² for 657 species to cross-validate the observed patterns of the modelled PD distribution results: a mean pair-wise rate of turnover between all pairs of cells within each time period, summarized using the mean and standard deviation for each year; and the rate of phylogenetic turnover from the present to each modelled time period for each cell.

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