

1 **Phylogenetic approaches reveal biodiversity threats under climate change**

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26 **Predicting the consequences of climate change for biodiversity is critical to conservation**  
27 **efforts<sup>1,2,3</sup>. Extensive range losses have been predicted for thousands of individual**  
28 **species<sup>4</sup>, but less is known about how climate change might impact whole clades<sup>1</sup> and**  
29 **landscape-scale patterns of biodiversity<sup>5</sup>. Here, we show that climate change scenarios**  
30 **imply significant changes in phylogenetic diversity and phylogenetic endemism at a**  
31 **continental scale in Australia using the hyper-diverse clade of eucalypts. We predict**  
32 **that within the next 60 years the vast majority of species distributions (91%) across**  
33 **Australia will shrink in size (on average by 51%) and shift south based on projected**  
34 **suitable climatic space. Geographic areas currently with high phylogenetic diversity and**  
35 **endemism are predicted to change substantially in future climate scenarios.**  
36 **Approximately 90% of the current areas with concentrations of paleo-endemism<sup>6</sup> (i.e.**  
37 **places with old evolutionary diversity) are predicted to disappear or shift their location.**  
38 **These findings show that climate change threatens whole clades of the phylogenetic tree,**  
39 **and can be used to forecast areas of biodiversity losses and continental scale impacts of**  
40 **climate change.**

41 By combining species distribution models (SDMs) with measures of evolutionary  
42 diversity, we can predict how climate change might impact the tree of life in the future<sup>1,7,8</sup>.  
43 Preserving the tree of life is increasingly recognised as an important consideration for  
44 conservation in Australia; globally, this evolutionary heritage provides a storehouse of  
45 unanticipated benefits for future generations, and locally it helps ensure resilient ecosystems  
46 and ongoing delivery of their services<sup>9,10,11,12</sup>. The most commonly used metric to quantify  
47 the diversity represented by the tree of life is phylogenetic diversity (PD), which represents  
48 the shared evolutionary history of species present in a region and is measured as the sum of  
49 branch lengths in the phylogenetic tree linking the species present<sup>10</sup>. PD does not include  
50 information on rarity of lineages, which is another important concern for conservation

51 priorities. Phylogenetic endemism (PE) addresses this problem by incorporating the degree of  
52 spatial restriction of phylogenetic branches found in an area, relative to all other areas<sup>13</sup>. This  
53 useful property means that PE can be used to identify areas that host relatively unique  
54 diversity, such as range-restricted "long branch" lineages (i.e., *paleoendemics* - species or  
55 clades with no living close relatives such as the reptile Tuatara, *Sphenodon*, or the fish  
56 Coelacanth, *Latimeria*).

57 In addition to preserving past evolutionary heritage, protecting areas that hold rapidly  
58 diversifying, range-restricted lineages (i.e., *neoendemics*) is a priority, because those lineages  
59 hold the key to future evolutionary potential. Previous studies have considered how climate  
60 change will impact the evolutionary heritage represented by PD<sup>1,7,8</sup>. PD is expected to be  
61 correlated with species richness. Therefore we applied a spatial randomization to evaluate  
62 departures of PD and PE from expectations<sup>6</sup>. Consequently, our PD-based metrics are  
63 decoupled from their corresponding species-based metrics. Here we present the first analysis  
64 describing how both the past and future of evolution might be impacted by climate change  
65 using model predictions and newly-developed phylogenetic metrics that take into account  
66 relative branch lengths.

67 We explored our approach for a key taxonomic group, Australian eucalypts (genera  
68 *Eucalyptus*, *Corymbia*, and *Angophora*). Australian eucalypts are an appropriate biological  
69 model because they are a hyper-diverse group (> 800 species) that dominate forest canopies  
70 and ecosystems across much of the continent. Eucalypts are mostly endemic to Australia and  
71 have a broad biogeographical diversity<sup>14</sup>. They are of global interest due to their widespread  
72 use in forestry<sup>15</sup>. They form a monophyletic lineage within the Myrtaceae family<sup>16,17,18,19</sup>,  
73 including the few eucalypt species that occur outside of Australia. Here we examine the  
74 expected shift in the geographic ranges of 657 species of eucalypt across Australia,  
75 comparing present ranges to those under forecast climate change scenarios for the years 2025,

76 2045, 2065 and 2085. We used SDMs to predict changes in geographic ranges and the  
77 direction in which ranges are likely to shift under future climate scenarios. SDMs have  
78 limitations when predicting responses to climate change<sup>20</sup> in species (e.g., climatic  
79 adaptability) and communities (e.g., species interactions). We accounted for some of the  
80 well-known weaknesses of SDMs by explicitly considering spatial bias and over-fitting, and  
81 comparing models with and without dispersal. The dispersal and non-dispersal scenarios  
82 produced very similar patterns, so we report only the results from the dispersal scenario.

83 Our study's novel findings regarding effects of climate change on phylogenetic  
84 diversity are grounded in our descriptions of impacts at the species level that corroborate  
85 previous findings. Eucalypt species are known to be threatened by climate change in  
86 Australia with previous results suggesting 53% of all *Eucalyptus* species predicted to be  
87 outside of their current climate conditions by 2070 under a 3°C warming scenario<sup>21</sup>. More  
88 recent SDM modelling for eucalypts suggests species ranges across the continent will  
89 contract and shift in both lateral and poleward directions, and the central desert areas will be  
90 particularly affected<sup>22</sup>. Our models predicted that by 2085, the current geographic range of  
91 91% of the 657 eucalypt species will shrink by an average of 51%, with 2.4% of species  
92 predicted to become extinct because their climate space will disappear entirely. Relatively  
93 few species (9%) are predicted to expand their geographic range (Fig. 1; see also SI\_2 for  
94 range size, % change, type of shift, shift magnitude and shift direction; and SI\_4 for maps for  
95 each of the 657 species).

96 To understand how these losses in species will manifest as changes in evolutionary  
97 diversity across the landscape, we calculated present and future PD<sup>10</sup> and PE<sup>13</sup> for all grid  
98 cells (~25km × 25km). These analyses predict that on average 2% of PD (decline in PD grid  
99 cells) will be lost across Australia by 2085 (Extended Data Fig. 1). Losses will occur in  
100 places recognised as national<sup>14</sup> and global biodiversity hotspots<sup>23</sup>. Additionally, we found that

101 the rate of turnover of PD increases over time, with a higher proportion of major changes  
102 occurring in southern Australia (Extended Data Fig. 9). Specifically, Mediterranean,  
103 temperate, and grassland ecosystems will face the greatest proportional change in clades  
104 present over time. This trend is accompanied by an increasing homogenization over the  
105 landscape. The average rate of phylogenetic turnover between all pairs of cells within a given  
106 year will decrease from 0.58 in the present to 0.50 in 2085 (Extended Data Table 1),  
107 suggesting an increase in average spatial homogeneity of phylogenetic composition (or  
108 phylogenetic homogenization) in the future. This spatial homogenization of PD has been  
109 documented previously for diverse groups in Europe<sup>1</sup>, and is suggested by past and current  
110 climate-driven plant extinctions for Thoreau's woods in the US and some temperate tree  
111 floras in Europe<sup>24,25</sup>. Here, for the first time, we show the potential effects of climate-change  
112 leading to PD loss in the future for a significant biological group of the southern hemisphere.

113 In contrast, PE is predicted to increase spatially in some of the areas of key diversity  
114 hotspots. In general, species endemism and PE are measures of rarity, and therefore,  
115 endemism tends to increase in the areas that hold the remaining portions of species ranges.  
116 The increase in PE is a result of lineages becoming more range-restricted. For example, in  
117 southwestern Western Australia, an internationally recognized biodiversity hotspot, species  
118 are predicted to retract toward the coast causing some coastal cells to have high PE in the  
119 future (Extended Data Fig. 1e). Predicting the location of high PE areas in the future is  
120 important from a conservation standpoint because these locations are likely to be the sites of  
121 concentrations of rare elements of diversity in the future, and, therefore, will be strategic  
122 areas for preventing further PD losses.

123 Two derived metrics, relative phylogenetic diversity (RPD) and relative phylogenetic  
124 endemism (RPE)<sup>6</sup>, can be used to better understand anticipated impacts on unusually long or  
125 short branches. These metrics reveal information about the underlying evolutionary processes

126 that we seek to understand and conserve<sup>6</sup> and also because they store old and highly unique  
127 lineages that, once lost, will significantly reduce the breadth of biodiversity. Sites with many  
128 very long branches are important repositories of unique evolutionary history and trait  
129 diversity<sup>26</sup>; sites with many short branches might indicate places with the potential for  
130 generating evolutionary adaptation and speciation in the future.

131         The RPD and RPE metrics reveal these patterns through an assessment that asks  
132 whether the contribution of unusually long or short branches to PD or PE in a grid cell is  
133 greater or less than expected by chance. RPD (or RPE) is the ratio of PD (or PE) measured  
134 using the set of species in that grid cell on the observed tree of the 657 eucalypt species to  
135 that measured on a comparison tree with the same topology but with all branches adjusted to  
136 be of equal (average) length<sup>6</sup>, with significant large or small ratios determined by a spatial  
137 randomization test (see Methods for details of randomization test)<sup>27</sup>. We find both areas of  
138 significantly high and significantly low RPD are predicted to decline in size (~10%) by 2085  
139 (Extended Data Fig. 2), indicating that unusually long- and short-branch lineages will  
140 disappear within sites.

141         Endemism can result either from younger lineages that have yet to expand their range  
142 or from older lineages that are relicts of a previously broader distribution. RPE allows the  
143 identification of centres of paleo-endemism (range-restricted long branches), centres of neo-  
144 endemism (range-restricted short branches), or both (centres of mixed endemism, termed  
145 "super endemism"), through a recently-developed method called CANAPE (Categorical  
146 Analysis of Neo- And Paleo-Endemism; see methods)<sup>6</sup>. We find that the current areas of  
147 paleo-, neo-, and super-endemism are predicted to significantly shrink (~50%) in size by  
148 2085 (Fig. 2; Extended Data Fig. 3a-e). This suggests that current areas of significant  
149 phylogenetic endemism may decline as lineages either go extinct or move to different  
150 locations (Figs. 2 and 3) with climate change.

151 Areas of paleo-endemism are particularly impacted;  $\geq 90\%$  of the current areas with  
152 significantly high paleo-endemism will disappear or shift to new places by 2085 (Fig. 2  
153 ellipses). Most of the large loss of paleo-endemism is due to shrinking geographic range of  
154 lineages (Extended Data Fig. 4). This large loss of paleo-endemism is a loss in the number of  
155 grid cells falling into that category. Shrinking ranges can increase the paleo-endemism of a  
156 cell that retains those long branches, but overall decreases of paleo-endemism areas reflects  
157 the loss of those branches from areas. For example, between the present and 2085, 64.6% of  
158 species' geographic ranges within current paleo-endemism areas will shrink (Extended Data  
159 Fig. 4), thus impacting their contribution to overall PE of these areas. There are currently 73  
160 grid cells with significant eucalypt paleo-endemism in Australia, containing 240 species. By  
161 2085, 52 of these species are predicted to go extinct or migrate elsewhere (Fig. 3).  
162 Consequently, most of these grid cells will cease to be areas of paleo-endemism by 2085.  
163 Declines of paleo-endemic areas tended to be even larger in the no-dispersal scenario, which  
164 otherwise gave similar results to the dispersal scenario reported in the text (Extended Data  
165 Fig. 3 f-j). These results show that areas of paleo-endemism are not necessarily places of  
166 long-term stability, but instead may be highly threatened and mobile.

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

172 Lineages are also predicted to disappear from places where new concentrations of  
173 paleo-endemism will form (see the square in central Australia and the larger rectangle in the  
174 far top-left in Fig. 2b). These sites currently contain 70 and 57 species and we predict that

175 23.3% and 7% of those species, respectively, will be locally extinct by 2085 (Fig. 2;  
176 Extended Data Fig. 5c, d).

177 Overall, the extinction of whole lineages is likely to occur as a result of severe  
178 reductions of climatic space (Extended Data Fig. 5a-d; and species list in SI\_1, Tables 1-4).  
179 The effect on the phylogeny was not evenly distributed as has been previously reported in  
180 some cases<sup>24</sup>, and we identified potential extinction of five species of *Eucalyptus* in  
181 Southwest Australia and three of *Corymbia* in southeast Queensland. This could be  
182 considered as an early sign of phylogenetic extirpation<sup>25</sup> or extinction of lineages of eucalypts  
183 (Fig. 3).

184 Few studies have addressed the impact of climate change on PD<sup>28</sup> and ours is the first  
185 to take the additional step of showing how climate change might affect PE including centres  
186 of paleo- (old) and neo- (young) -endemism across a continental-scale landscape. Our  
187 approach can be considered as an early warning system for forecasting biodiversity loss  
188 across the landscape, critically expressed as loss of evolutionary heritage and evolutionary  
189 potential. Here we show that the contraction of lineage ranges expected with climate change  
190 is likely to reduce diversity at most locations, homogenise the landscape, and particularly  
191 impact rare long- and short-branch lineages, which might cause significant losses to the tree  
192 of life and reduce genetic adaptive potential of eucalypts under climate change<sup>29,30</sup>. Faced  
193 with substantial losses to biodiversity with climate change, our approach allows the  
194 identification of areas that are key to preventing further biodiversity loss.

195 Specifically, we found major shifts in eucalypts' modelled distributions which, if  
196 realized, would lead to a shrinkage of current areas of high phylogenetic endemism for the  
197 species group along all the southwest, southeast, and southern coastal regions of Australia.  
198 We find that Tasmania, due to its lower latitude and more temperate climate, might become a  
199 very important refugium, while Victoria is more prone to losing areas of neo-endemism.



200 Current hotspots of paleo-endemism in southeast Queensland, northern coastal NSW, and  
201 central Australia are also predicted to be impacted severely. Conversely, new concentrations  
202 of paleo-endemism are predicted to occur in the Kimberley and northern coastal region  
203 demonstrating the potential of our methods to identify key areas that might be important  
204 refugia in the future.

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282 **Supplementary Information** is available in the online version of the paper

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**Acknowledgements**

We acknowledge the National Environmental Research Program (NERP) for workshop funding, the Bjarne K Dahl Trust for support, and the ARC grant DP130101141 for supporting the eucalypts phylogenetic work. BDM acknowledges a Visiting Fellowship from the Collaborative Research Network for Murray-Darling Basin Futures, University of Canberra in 2013. This manuscript includes work done by JTM while serving at the National Science Foundation. The views expressed in this paper do not necessarily reflect those of the National Science Foundation or the United States Government.

**Author contributions**

All authors contributed to project conception. C.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.G-O, L.J.P and N.B compiled and corrected species spatial data records. C.G-O wrote the manuscript draft and all authors contributed to interpretation of the results and writing of the final paper.

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## Methods

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### 312 Spatial Data and Species Distribution Modelling

313 We modelled present and future distributions of current and four future time points  
314 (2025, 2045, 2065 and 2085) for all 766 eucalypt species (~163,000 occurrence records)  
315 found in Australia (only 16 are endemic to another country) at a 5-km pixel resolution using a  
316 dispersal and a no-dispersal scenario. Data (presence-only) were extracted from Australia's  
317 Virtual Herbarium database [AVH] accessed in October 2011 (<http://avh.chah.org.au/>).  
318 Species names were rectified using the current species list found in Euclid Version 3.0<sup>31</sup> and  
319 experts were consulted in particular cases when naming history was difficult to reconstruct.  
320 Latitudinal biases were corrected by spatial geo-rectifications. Points outside the known  
321 natural range were removed for each species based on range maps and expert opinion, and  
322 pre-1950 records were removed to limit spatial uncertainty<sup>32</sup>.

323 We used the Representative Cost Pathway (RCP) 6.0 scenario for the Hadley global  
324 climate model (hadcm3, <http://wallaceinitiative.org/>). We focused on this moderate climate  
325 scenario because of its fit with the Australian strategy on emission reductions, and because  
326 the literature suggests that eucalypts will be significantly affected under a 3°C warming by  
327 2070<sup>21</sup>. Strictly our predictions are therefore only valid for this scenario, but as it is an  
328 intermediate scenario our predicted responses are most likely also of the intermediate type. In  
329 case there is a reason in the future to suggest a different scenario to be more likely our  
330 approach can be easily adapted to such a scenario. We used a simplified set of predictor  
331 variables that we believe to be physiologically relevant (maximum temperature and dry  
332 season rainfall) with strong predictive power<sup>22</sup>, spatial variables (latitude and longitude) and  
333 one edaphic variable (median % clay content derived from the 1:2 M Atlas of Australian  
334 Soils<sup>33,34</sup>). Spatial predictors were included in the models because they help constrain the

335 modelled distributions to a more realistic spatial extent based on an initial trial of 20 species  
336 with good distribution data.

337         The AVH dataset is heavily influenced by road-based sampling, which was accounted  
338 for by including distance-to-roads as a predictor in each model, then setting distance-to-roads  
339 to zero for prediction (for present and future scenarios). Models were fitted using MaxEnt<sup>35</sup>  
340 in the R package ‘dismo’ with a random background sample of 20,000 records (the same  
341 sample for each species), randomly distributed across Australia and uniform for all species.  
342 We used only ‘hinge features’ because they tend to increase model performance without  
343 increasing model complexity<sup>36</sup>. Hinge features provide smoother response curves, which may  
344 more closely approximate the species’ fundamental niche<sup>37</sup>. Model fit was evaluated with  
345 Area Under the ROC Curve from a 5-fold cross-validation for each species (see AUC values  
346 in SI\_3). A Maxent logistic threshold (maximum training sensitivity plus specificity) for each  
347 species was applied to convert habitat suitability into presences and absences for present and  
348 future scenarios.

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

### 353 **Molecular data**

354 DNA data for the study was gathered by using existing and newly generated nuclear (ITS and  
355 ETS) and chloroplast sequences (*matK* and *psba-trnH*) that were successfully amplified for  
356 711 eucalypt species (See Table in SI\_5 for GenBank accessions). Leaves for DNA  
357 extraction were sourced from numerous field trips, botanical gardens, arboreta, and herbaria  
358 from multiple locations around Australia. In total 2560 gene sequences were used in the

359 study, 237 were mined from GenBank, and 2323 were newly generated for this project. These  
360 sequences represented the 711 eucalypt species and 21 taxa from other Myrtaceae tribes  
361 which were used to root the phylogeny (Extended Data Fig. 6). Individual locus alignments  
362 were constructed using Muscle<sup>38</sup> and adjusted manually in Se-AL<sup>39</sup>.

363 The phylogenetic analysis was performed on the concatenated alignment using  
364 maximum likelihood in the CIPRES Portal ([www.phylo.org](http://www.phylo.org)), utilising the RAxML HPC  
365 BlackBox tool with a partition model set for each locus, with bootstrapping set to  
366 automatically halt, which occurred after 550 replicates. The ML tree with bootstrap values is  
367 shown in Extended Data Fig. 7. Extended Data figure 8 is a bi-plot of branch length vs,  
368 bootstrap score, and shows that low bootstrap scores were restricted to very short branches.  
369 The uncertainty in these short branches did not affect the analyses presented here, since the  
370 better supported long branches contribute most of the PD.

### 371 **Species range shift analyses**

372 The mean centre of distributional area using the Maxent habitat suitability maps under  
373 present and future scenarios was estimated for the 657 species with matching phylogenetic  
374 data and SDMs following established methods<sup>40</sup>. This analysis showed the magnitude and  
375 direction of change of the mean centre of the climate space for each species between the  
376 present and 2085. Species were grouped according to their distribution change from the  
377 present, namely into “expanding” or “shrinking” if the predicted suitable climate space of a  
378 species increased or decreased between the present and 2085, respectively. Species whose  
379 suitable climate space was predicted to become extinct by 2085 were classified as  
380 “extinct”. The ‘dispersal’ scenario assumes all species can disperse across the landscape.  
381 However, the use of spatial variables in the models indirectly accounts for some dispersal  
382 limitation, effectively limiting the potential of species to disperse to distant sites. We believe



383 this spatial dispersal limitation is realistic given the biology of eucalypts, with most species  
384 having relatively heavy seeds without specialized dispersal mechanisms that simply drop to  
385 the ground when shed. Given the tree height, seed weights, and average wind speeds, most  
386 eucalypt species would not be expected to disperse beyond a single grid cell during the time  
387 period in this study without a rare long-distance dispersal event<sup>41</sup>.

### 388 **Spatial phylogenetic analyses of modelled distributions**

389 The SDM suitability values were aggregated at  $\sim 25\text{km} \times 25\text{km}$  to a total of 12,813 grid cells  
390 and used to calculate Species Richness (SR), Weighted Endemism (WE), Phylogenetic  
391 Diversity (PD)<sup>10</sup>, Phylogenetic Endemism (PE)<sup>13</sup>, Relative Phylogenetic Diversity (RPD) and  
392 Relative Phylogenetic Endemism (RPE) in the Biodiverse software<sup>42</sup> for 657 species. SR and  
393 WE results reported in Extended Data Fig. 1 were calculated on the basis of all 766 species  
394 because they did not require a phylogenetic tree. All phylogenetic metrics were calculated on  
395 the basis of the 657 species that are in the phylogeny. A spatial randomization based on 999  
396 trials was applied to these metrics<sup>6</sup>. The purpose of the randomization is to identify whether  
397 the observed values were significantly different from a random selection of the same number  
398 of terminal taxa from the tree.

399 RPE is applied in a two-step test called categorical analysis of neo- and paleo-  
400 endemism (CANAPE) using the same spatial randomization<sup>6</sup>. The first step of CANAPE  
401 determines whether a location is a center of high phylogenetic endemism by applying a one-  
402 tailed test (for large values) to both the numerator and denominator of RPE (i.e., PE measured  
403 on the observed tree in the numerator and PE measured on a comparison tree where all  
404 branches are of equal (average) length in the denominator). Then, for grid cells passing this  
405 test, the second step applies a two-tailed test to the RPE ratio to identify cells dominated by  
406 unusually short range-restricted branches (centres of neo-endemism), unusually long range-

407 restricted branches (centres of paleo-endemism), or both (centres of mixed endemism, termed  
408 "super endemism" if both the numerator and denominator of RPE are highly significant)<sup>6</sup>.

#### 409 **Phylogenetic turnover analyses of modelled distributions**

410 Two spatial turnover analyses using the Phylo Sørensen index<sup>43</sup> were conducted in  
411 Biodiverse<sup>42</sup> for 657 species to cross validate the observed patterns of the modelled PD  
412 distribution results: (1) a mean pair-wise rate of turnover between all pairs of cells within  
413 each time period, summarised using the mean and standard deviation for each year; and (2)  
414 the rate of phylogenetic turnover from the present to each modelled time period for each cell.

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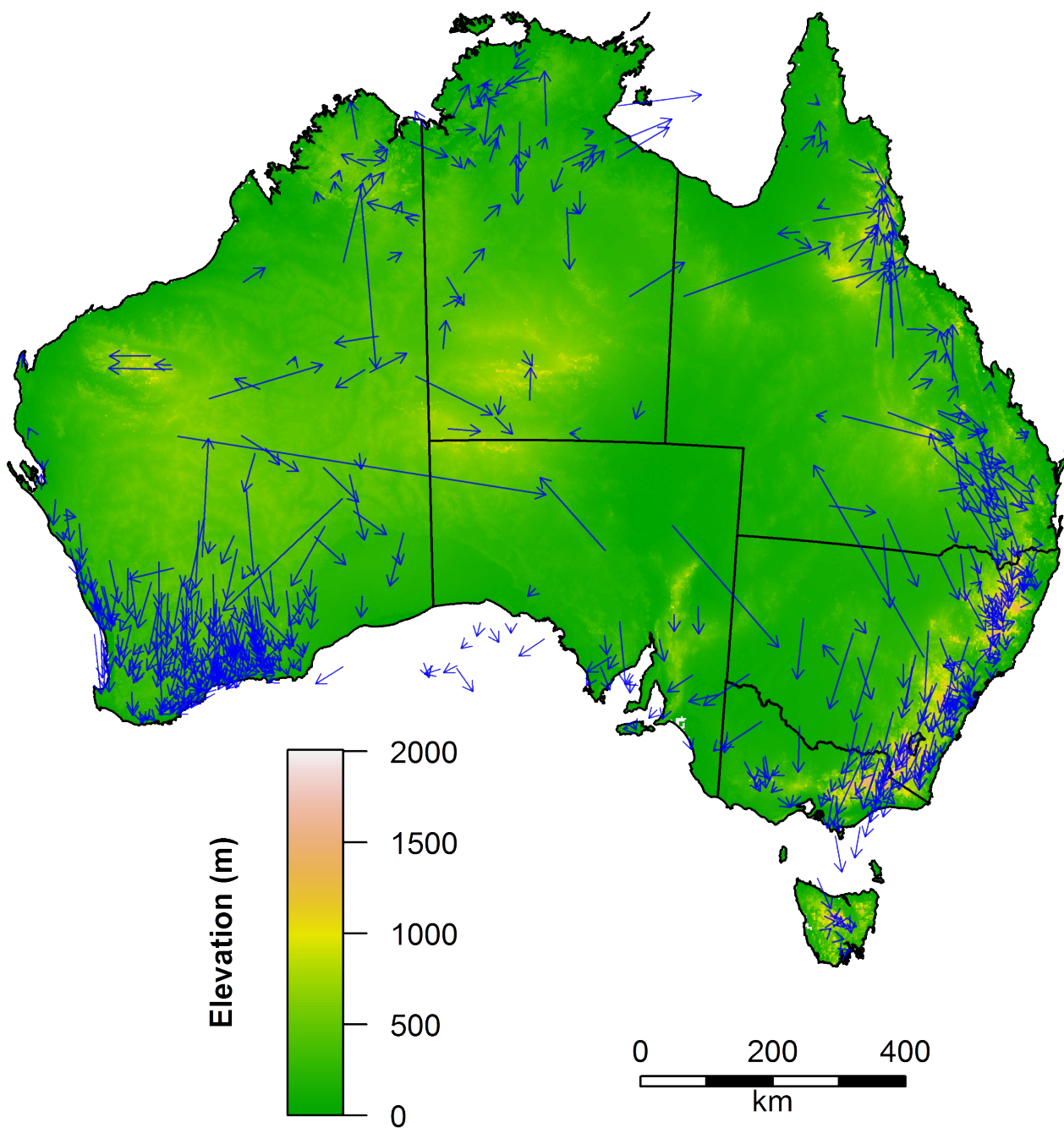
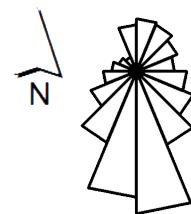
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## Figures legends

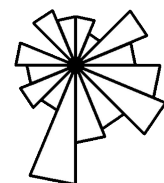
455 **Figure 1 | Variation in the predicted distribution of the suitable climate space of 657**  
456 **Australian eucalypt species from 2014 to 2085. a,** Shift in the predicted species  
457 distribution where arrows present the magnitude and direction of change in distribution at the  
458 centroid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

461 **Figure 2 | Areas of phylogenetic endemism using Categorical Analysis of Neo- And**  
462 **Paleo-Endemism (CANAPE) for 657 species of eucalypts in Australia for projected**  
463 **climate change scenarios at 2014 and 2085. a,** CANAPE map for 2014, and **b,** 2085.  
464 Ellipses indicate places where current areas of paleo-endemism disappear; rectangles indicate  
465 places where new areas of paleo-endemism appear; triangles indicate where current areas of  
466 paleo or neo-endemism weaken. Beige areas do not depart significantly from random  
467 expectation.

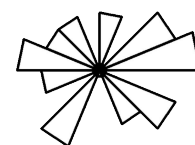
468 **Figure 3 | Effects of projected climate change scenarios, between 2014 and 2085, on**  
469 **species of eucalypts found in current areas of paleo-endemism across Australia.**  
470 **Highlighted branches in the phylogenetic tree are present in the 73 grid cells that had**  
471 **significant paleo-endemism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

**a****b**

shrinking  
N=580



expanding  
N=61

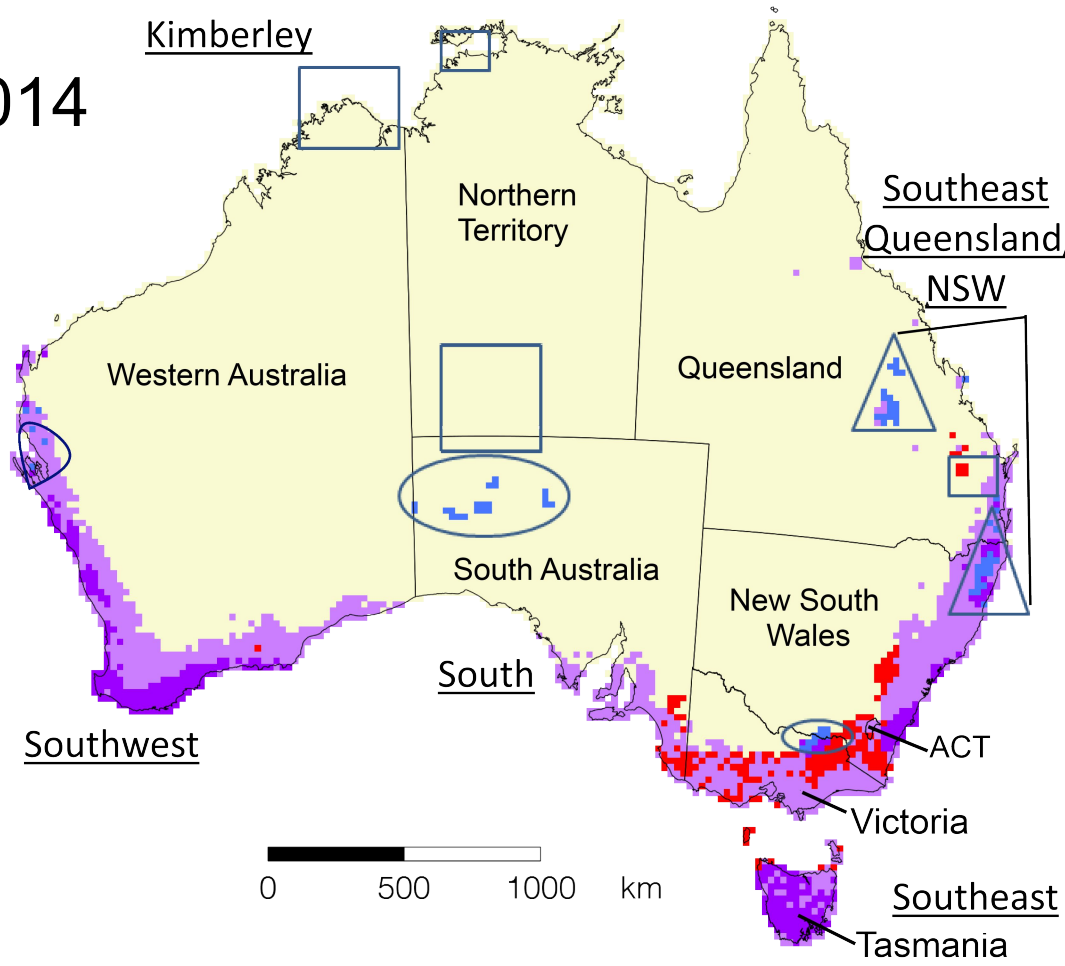


extinct  
N=16

# Categorical Analysis of Neo- And Paleo- Endemism

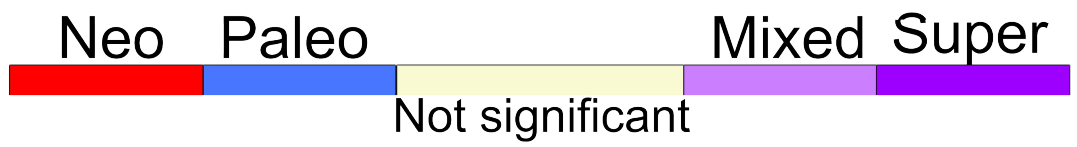
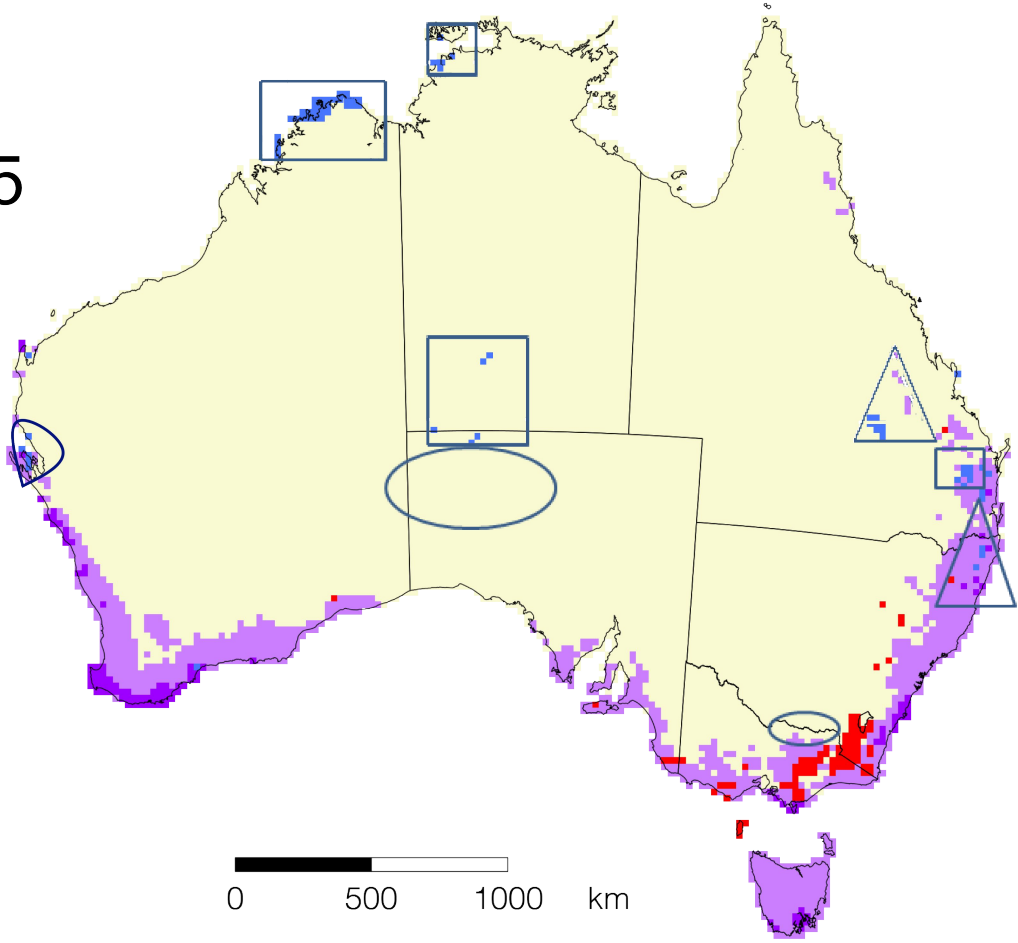
**a**

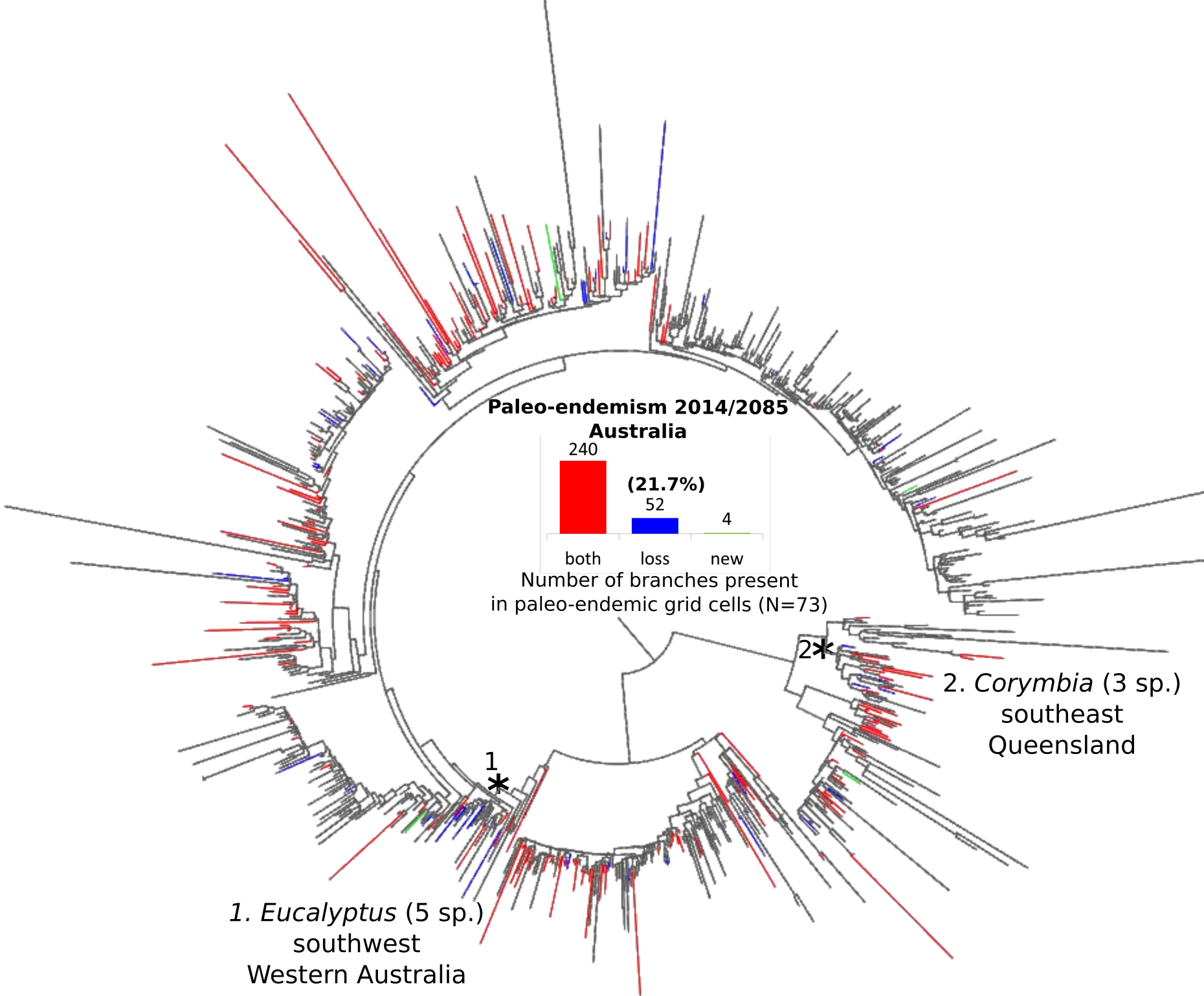
2014



**b**

2085





0.03