Projecting Podocarpaceae response to climate change: we are not out of the woods yet

Thando C. Twala (thando.twala@wits.ac.za)
University of the Witwatersrand
Jolene T. Fisher
University of the Witwatersrand
Kelsey L. Glennon
University of the Witwatersrand

Research Article

Keywords: Climate change, environmental niche, persistence, Podocarpaceae, species distribution

Posted Date: June 9th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1725513/v1

Additional Declarations: No competing interests reported.

Title

Projecting Podocarpaceae response to climate change: we are not out of the woods yet

Author Information

Thando C. Twala[1,*], Jolene T. Fisher[1], and Kelsey L. Glennon[1]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Johannesburg WITS 2050, South Africa

[*]corresponding author email: thando.twala@wits.ac.za ; +27 65 936 6293

Acknowledgements

This research was funded by the National Research Foundation grant to J. T. Fisher (Grant No: 117983), by a National Research Foundation Innovation Scholarship to T. C. Twala (Grant: 117767), and by a Friedel Sellschop Award to K. L. Glennon.

Abstract

Under the changing climate, the persistence of Afrotemperate taxa may be threatened as suitable habitat availability decreases. The unique disjunct ranges of podocarps in southern Africa raise questions about the persistence of these species under climate change. Here, we identified likely environmental drivers of these distributions, characterised the current and future (2070) environmental niches, and projected distributions of four podocarp species in South Africa. Species distribution models were conducted using species locality data for *A. falcatus, P. latifolius, P. elongatus* and *P. henkelii* and both historical climate data (1970 – 2000) and future climate scenarios (RCP 4.5 and 8.5, 2061 – 2080) to estimate the current and future distributions. We also used this opportunity to identify the most important climatic variables that likely governed each species' distribution. Using niche overlap estimates, a similarity test, and indices of niche expansion, stability and unfilling, we explored how niches changed under different climate scenarios. The distribution of the study species was governed by max temperature of the warmest month, temperature annual range, mean temperature of the wettest quarter, and precipitation of the wettest, driest, and warmest quarters. The current distribution of *A. falcatus* was predicted to expand to higher elevations under RCP 4.5 and RCP 8.5. *Podocarpus henkelii* was predicted to lose most of its suitable habitat under RCP 4.5 and expand under RCP 8.5, however this was the opposite for *P. elongatus* and *P. latifolius*. Interestingly, *P. elongatus,* which had the smallest geographic distribution, showed the most vulnerability to climate change in comparison to the other podocarps**.** Mapping the distribution of podocarps and understanding the differences in their current and future climate niches provides insight into potential climate drivers of podocarp persistence and the potential for adaptation of these species. Overall, these results suggest that *P. elongatus* and *P. henkelii* may expand to novel environmental niches.

Keywords: Climate change, environmental niche, persistence, Podocarpaceae, species distribution

1. Introduction

Conifers are a crucial component of global forests with both economic and ecological importance (Farjon 2018). Podocarpaceae (podocarp) is the second most species rich conifer family and the largest clade in southern conifers with 19 genera and 187 species (Christenhusz and Byng 2016) and are one of the few gymnosperms that inhabit tropical forests in the Southern Hemisphere. Species in the Podocarpaceae were historically centered in Gondwana, subsequently expanding to Australasia and southernmost South Africa and current occur in Malaysia. They were prominent in Gondwana during the Cretaceous period (Krassilov 1974) diversifying by the early Triassic period into the podocarps we know today. This diversification is possibly due to the onset of warmer and wetter climates because of the opening of the South Ocean (Atlantic and Indian Ocean). During the mid-Cretaceous, podocarps went extinct in West Africa during the flattening of the uplands, reduced in extent in India during the late Cretaceous when it drifted northwards (Morley 2000), and dispersed into its current Southeast Asian distribution following global cooling. In Africa, global cooling may have enabled the dispersal of podocarps from East Africa to the highlands of West Africa. As a result, podocarps display a largely pantropical distribution, although extending into subtropical and temperate latitudes, where they mainly occur in Australasia, central and South America and tropical montane Africa (Farjon 2010; Klaus et al. 2020).

Climate change and competition with angiosperms have been some of the most important factors that influence podocarp distribution and persistence (Quiroga and Premoli 2007; Migliore et al. 2022). Podocarps appeared to respond to these threats through either dispersal into favourable climate conditions or subsequent adaptation to less favourable conditions but may have also used both means to evade potential threats. As a result, podocarps show remarkable adaptability in habitat, growth form and physiological traits. For instance, some members of the family are semiaquatic (*Retrophyllum minor* (Carriére) C.N.Page), parasitic (*Parasitaxus usta* (Vieill.) de Laub.), exhibit resprouting and fire and drought tolerance (*Podocarpus drouynianus* F.Mueller. and *P. spinulosus* R.Br. ex Mirb.), shade tolerance (*P. latifolius* (Thunb) R.Br. ex Mirb.), tolerance to soil anoxia (*Manoao colensoi* (Hook.) Molloy), diverse fleshy seed cones (*P. elongatus* E.Mey. ex Endl*, Afrocarpus falcatus* (Thunb.) C.N.Page*),* diverse leaf morphology (*P. nagi* (Thunb) Pilg., *P. henkelii* Stapf ex Dallim. & Jackson*, P. macrophyllus* (Thunb.) Sweet), leaf and individual longevity, and have conspicuous root nodules which house arbuscular mycorrhiza fungi (Molloy 1995; Hill and Brodribb 1999; Biffin et al. 2012, Contreras et al. 2017). The symbiotic relationship between podocarp plant roots and fungi (Glomeromycota) increased the ability of podocarps to acquire phosphorus, which enabled podocarps to colonise nutrient poor environments (Yeager and Johnson 1985). Remarkably, most podocarps are restricted to humid, mountainous environments, including angiosperm-

dominated forests. In Afrotemperate forests, podocarps persist within fynbos, heathland, or grassland matrices where fire and grass competition are the predominant factors that influence forest distribution (Adie and Lawes 2009a; Adie and Lawes 2011; Adie et al. 2017). As many extant podocarps are slow growing, fire and drought intolerant, this put them at a competitive disadvantage when co-occurring with angiosperms (Bond 1989; Brodribb and Hill 1998), which restricts them to these stepping stone refugia.

Developing management strategies and practical measures to conserve podocarps will be difficult without knowing the environmental variables that are key to each species' climatic niche and predicted geographical distribution under future climate conditions. Moreover, climate change affects habitat requirements for many species (Bakkenes et al. 2002; Aitken et al. 2007; Essl et al. 2011; Moran 2020; Fricke et al. 2022). Consequently, determining whether climate change will affect the geographical distribution and environmental niches of podocarps presents another critical challenge linked to their ecological value and significance. The current distributions of *Afrocarpus falcatus, Podocarpus elongatus, Podocarpus henkelii* and *P. latifolius* are relatively well known; however, little is known about the environmental drivers of podocarp distribution, their dispersal patterns and how climate change will affect their distribution and environmental niches. In this study, we used a combined environmental (niche overlap indices) and geographical approach (temporal transferability of SDMs) to characterise the distribution and environmental niche of *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius*. The objectives of this study were to (1) identify the environmental variables that shape the distribution of *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius*; (2) model the current distribution of South African podocarps; (3) project the current models onto future climate emissions scenarios; and (4) compare the future geographic distribution of podocarp environmental niches to their current environmental niche geographic distribution. Such comparisons will enable us to infer the vulnerability of these South African podocarps to variations in the changing environment.

2. Methods

Generally, our study included three major steps, with relevant details reported below: (i) data were downloaded, compiled and variables were selected, (ii) *A. falcatus, P. elongatus, P henkelii* and *P. latifolius* occurrence and climate data were used to characterise niche and environmental spaces, and (iii) a variety of species distribution modelling algorithms were used to project the potential distribution of *A. falcatus, P. elongatus, P henkelii* and *P. latifolius* in South Africa.

2.1. Study species

In Africa, podocarps are restricted to highland archipelagos in montane forests along the Afromontane Forest belt, where they persist in small forest patches within a grassland, fynbos, or heathland matrix. The Afromontane Forest belt extends from Ethiopia along the eastern mountain range, all the way to the southern Cape in South Africa. *Afrocarpus falcatus* is present throughout Afromontane forests and is absent in West Africa. South Africa consists of four podocarp species from sister genera: *Afrocarpus* (*A. falcatus*) and *Podocarpus* (*P. elongatus, P. henkelii* and *P. latifolius;* Farjon 2001). *Afrocarpus falcatus* and *P. latifolius* are widely distributed geographically across South Africa but are restricted to Afromontane forest habitats. In South Africa, *A. falcatus* and *P. latifolius* occur along the southwest of South Africa and extend to the south and east coast of the country up the Drakensberg mountains in the eastern parts of the country and extend northwards in temperate midland regions towards Zimbabwe. *Podocarpus henkelii* occurs in forest habitats and is restricted to summer rainfall areas in the mesic east of the country. *Podocarpus elongatus* only occurs in the extreme western and southern parts of the country (winter rainfall) in the forest and fynbos biome.

2.2. Species occurrences

Afrocarpus falcatus, *P. elongatus, P. henkelii* and *P. latifolius* occurrence data were downloaded from the Global Biodiversity Information Facility online repository (GBIF; https://www.gbif.org/). Where necessary, location information was georeferenced and duplicate localities were removed. Records were validated using Google Earth v7.1.2 and outliers associated with non-natural locations were removed. After filtering, 562 localities were retained in the final analysis for all four species: *A. falcatus* (n = 246), *P. latifolius* (n = 242), *P. elongatus* (n = 49) and *P. henkelii* (n = 25; Figure 1).

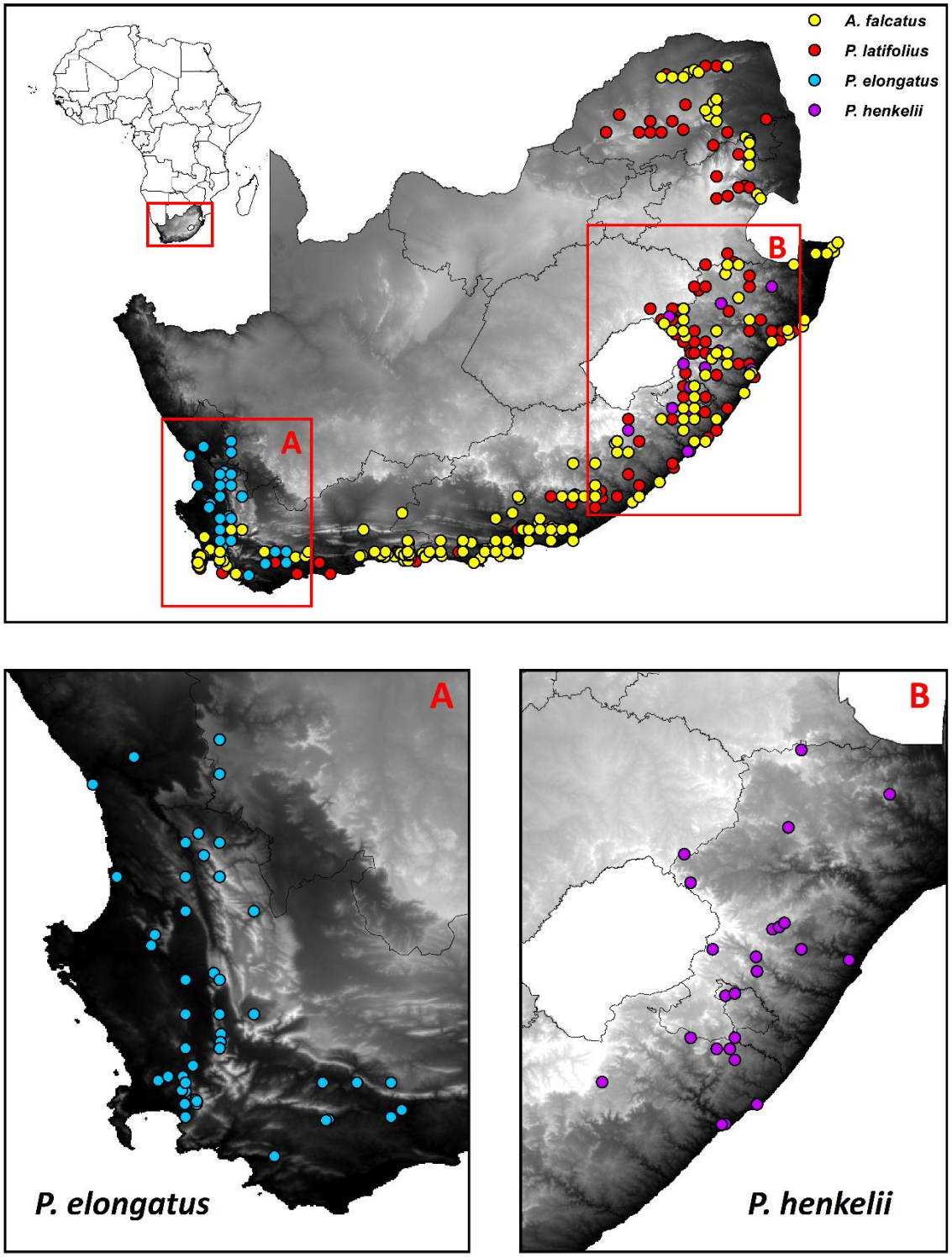


Figure 1. South African occurrences of *Afrocarpus falcatus, Podocarpus latifolius, P. elongatus* (inset A) and *P. henkelii* (inset B) that were downloaded from the Global Biodiversity Information Facility (http://gbif.org). The map is shaded according to elevation where darker grey indicates low elevation and light grey/white areas indicate high elevation (> 1800m.a.s.l).

2.3. Climate variables

Current climate data were downloaded from Chelsa version 2.1 (historical (1970 – 2000) and future (2061 – 2080) climate data were downloaded under Representative Concentration Pathways (RCP) 4.5 and 8.5 emission scenarios from the Hadley Global Environment Model 2-Atmosphere Ocean (HADGEM2-AO) circulation model. These data were downloaded using "Chelsa.CMIP_5.download" function from the *ClimDatDownloadR* R package (Karger et al. 2017; Jentsch et al. 2021). All environmental variables had a spatial resolution of 30 arc seconds (~1km^2 pixel area at the equator). To avoid obtaining spurious results and overparameterization of the models due to variable multicollinearity (Elith et al. 2010; Synes and Bsborne 2011; Boria et al. 2014), variable correlations were minimized using dimension reduction techniques. A Pearson's correlation test based on all 19 climate variables was conducted for all species presence points and used to exclude highly correlated variables ($r > 0.65$) from our models. Seven predictor variables were used in subsequent processing: Mean Temperature of Warmest Month (BIO05), Max Temperature of the Warmest Month (BIO05), Temperature Annual Range (BIO07), Mean Temperature of Wettest Quarter (BIO08), Mean Temperature of Coldest Quarter (BIO11), Precipitation of Wettest Quarter (BIO26), Precipitation of Driest Quarter (BIO017), and Precipitation of Coldest Quarter (BIO18).

2.4. Species distribution modelling (SDM)

Species distribution models (SDMs) are mathematical algorithms that estimate a species' climatic niche by characterising a species' occurrence in relation to environmental factors (Elith et al. 2006). SDMs can be used to analyse and predict patterns of distribution and could estimate the risk these environmental drivers pose to species as they quantify the relationship between plant distributions and environmental factors (Guisan and Thuiller 2005; Elith and Leathwich 2009; Wiens et al. 2010; Guisan et al. 2013); thus, demonstrating their vulnerability more accurately. Many assumptions of SDMs assume niche conservatism which suggests that species can maintain their environmental niches (Peterson et al. 1999; Wiens 2004; Peterson 2011). It is still controversial whether species' ecological niches are preserved in space and time (Peterson et al. 1999; Broennimann et al. 2007). As a result of the ongoing theoretical development and quantification of species' ecological niche, researchers have advanced our understanding of how species fluctuate in their requirements for and tolerance of various factors (Soberón 2007).

Species distribution modelling uses occurrence data and environmental variables to simulate suitable/habitable environmental conditions for focus species. Here, we used ten different

algorithms available within the *biomod2* package (Thuiller et al. 2021) in R version 4.1.1 to obtain an ensemble of predicted distributions: generalised linear model (GLM), generalised additive models (GAM), generalised boosting model/boosted regression trees (GBM), surface range envelop/BIOCLIM (SRE), classification tree analysis (CTA), artificial neural network (ANN), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS), random forest (RF) and maximum entropy (MAXENT). The following parameters were set for the models: one run of five hundred pseudo-absence points was used on one model evaluation, split into 80% for training and 20% for testing for each SDM, and variable importance was determined using three permutations for the full extent of South Africa. The remaining model values were set to default values. Area under the receiver operating curve (AUC), true skills statistics (TSS) and the continuous Boyce index (CBI) were used to assess model predictive efficiency and performance (Hanley and McNeil, 1982; Allouche et al. 2006). The Boyce index uses presence data only to measure how different the model predictions are from a random distribution of observed presence across the prediction gradient. Boyce index values range between -1 and +1, where positive values indicate that the model predictions are consistent with the presence data, values close to zero suggest that the model is no different from a random model, and negative values indicate no occurrence when there is. All statistical analyses were performed in R using scripts from Broennimann et al. (2012), which are now available in the *ecospat* R package (Di Cola et al. 2017; Broennimann et al. 2020).

The potential distribution for each species was projected under the Representative Concentration Pathway (RCP) 4.5 and RCP 8.5 future climate emission scenarios for the year 2070 (average for 2061 – 2080). Representative Concentration Pathways (RCP) are models of greenhouse emissions scenarios which predict future climate under different greenhouse emissions scenarios. Representative Concentration Pathway 4.5 and 8.5 were chosen because RCP 4.5 greenhouse gas emissions are projected to peak around 2040 and then decline, while in RCP 8.5 greenhouse gas emissions are projected to continue to increase throughout the 21st century, respectively a “best-case” and “worst-case” scenario (Meinshausen et al. 2011). At the current rate of emissions and mitigation processes these are the most likely scenarios. RCP 2.6 was not included because it was unrealistic, as it assumed peak emissions by 2020 and subsequent decline (Meinshausen et al. 2011).

Binary maps were generated from SDMs, and the current and future binary models were used to calculate the change in geographic area of *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius* between the current and future climate emissions scenarios. Changes in geographic area were classified as ‘loss’, ‘gain,’ and ‘stable’. Loss referred to the area the species originally occupied, but no longer occupies after climate change. Gain referred to occupied areas that the species did not

originally occupy and then occupy after climate change. Stable referred to areas that persisted after climate change, or also referred to as climatic microrefugia (Pang et al. 2021). All geographic information system analyses were done in ArcGIS v 10.8 (ESRI).

2.5. Calculating niche overlap in environmental space

Assessing climatic niche characteristics is a powerful approach for studying niche divergence and conservatism. Broennimann et al. (2012) presented a principal component analysis (PCA) method which places environmental variables into two-dimensional space identified by their first and second principal components. When testing niche divergence and niche conservatism hypotheses, niche overlap can provide a relatively reliable measurement of overlap. We quantified the degree of shared environmental niche space between the current and the future climate emissions scenarios of *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius*. In this study, niche overlap between current and future climate emissions scenarios for each podocarp species was computed using the Schoener's *D* statistic (Schoener 1968; Warrren et al. 2008). Schoener's *D* ranges from 0 (no overlap) to 1 (complete overlap). Results were then interpreted using the classification scheme suggested by Rödder and Engler (2011) where *D* ranges indicated potential interpretations: 0.0 – 0.2 = no or very limited overlap, 0.2 – 0.4 = low overlap, 0.4 – 0.6 = moderate overlap, 0.6 – 0.8 = high overlap, and 0.8 – 1.0 = very high overlap/identical niche. Subsequently, niche overlap was interpreted in the context of three general niche categories: niche expansion, stability/stasis and unfilling (Petitpierre et al. 2012; Glennon et al. 2014; Guisan et al. 2014; Di Cola et al. 2017). Niche stability (i.e., the proportion of the current range niche overlapping with the future range niche), niche expansion (i.e., the proportion of the future range niche not overlapping with the current range niche) and niche unfilling (i.e., the proportion of the current range niche not occupied in the future range niche) enables the ability to generate hypotheses about the potential drivers of podocarp niche dynamics between current and predicted climatic emission scenarios. The niche stability and expansion values always sum to 100%. The niche unfilling value corresponds to the expansion value when shifting current and future ranges. Niche conservatism is defined as the tendency for species to retain their environmental niche in space and time and is represented by "niche stability".

We also used an ordination technique that applies kernel density smoothers to species presences in environmental space (Broennimann et al. 2012) to determine the environmental niche occupied by each species under current and future climate emissions scenarios. The kernel density function is applied for smoothing the density of occurrences for each of the generated grid cells, which correspond to the vector of the available environmental conditions in the study area under

each climate emission scenario. This smoothing approach removes any biases to obtain a better representation of the environmental conditions suitable for each species under current and future climate emissions scenarios. This approach was implemented using a principal component analysis which is an ordination technique that is calibrated on the entire environmental space based on the focal variables of both current and future climate emission scenarios (hereafter referred to as PCA-env). Further details can be found in Broennimann et al. (2012).

We also performed the niche similarity test, which assesses if the environmental niches of each species are more similar or more dissimilar than expected by chance in comparison to each other under current and future climate scenarios, accounting for differences in the surrounding areas of the localities (background space) under current and future climate emissions scenarios (Warren et al. 2008; Warren et al. 2010; Warren et al. 2018). The niche similarity test compares the niche overlap of one species range randomly distributed over its background, while keeping the other unchanged (e.g., Current: *A. falcatus* → *P. elongatus*), and then carries out the reciprocal comparison (e.g., Current: *P. elongatus* → *A. falcatus*). For the niche similarity test, an alpha value of 0.05 was considered to indicate that niches were no more similar than expected by chance.

3. Results

3.1. Model evaluation indices

We calculated the commonly used (AUC) and the less commonly used (TSS and CBI) model evaluation indices. Model performance was good for all the emission scenarios (Table 1). AUC varied from 0.990 to 0.992, TSS varied from 0.681 to 0.978. The CBI suggested that all the model predictions were consistent with the distribution of the actual data as they all had positive CBI values. However, CBI values for *P. elongatus* under the current emission scenario was close to zero.

Table 1. Area under the ROC curve (AUC) and true skills statistics (TSS) values showing species distribution model performance and continuous Boyce index (CBI) showing how well the models fit the presence data of *Afrocarpus falcatus, Podocarpus latifolius, P. elongatus* and *P. henkelii* current and future climate emissions scenarios (RCP 4.5 and 8.5) in their South African distribution.

Species	Emission scenario	AUC	TSS	CBI
A. falcatus	Current	0.961	0.834	0.818
	RCP 4.5	0.958	0.814	0.806
	RCP 8.5	0.955	0.795	0.943
P. elongatus	Current	0.992	0.978	0.250
	RCP 4.5	0.990	0.940	0.889
	RCP 8.5	0.992	0.957	0.911
P. henkelii	Current	0.978	0.954	0.529
	RCP 4.5	0.945	0.858	0.732
	RCP 8.5	0.967	0.909	0.754
P. latifolius	Current	0.942	0.738	0.854
	RCP 4.5	0.918	0.681	0.894
	RCP 8.5	0.920	0.690	0.868

3.2. Importance of environmental variables

The current distribution of *A. falcatus* is determined by precipitation of the driest quarter (BIO17; **Current importance vale (IV):** 0.455; Table 2). Temperature annual range (BIO07) was the most important variable constraining the future distribution of *A. falcatus* (**RCP 4.5 IV:** 0.607; **RCP 8.5 IV:** 0.554) and *P. latifolius* (**RCP 4.5 IV:** 0.542; **RCP 8.5 IV:** 0.585). Precipitation of the driest quarter (BIO17) and precipitation of the wettest quarter (BIO16) were the most important variables shaping the current distribution of *A. falcatus* and *P. latifolius*, respectively. Precipitation of the warmest quarter (BIO18) was predicted to be the most important variable constraining the current and future distributions of *P. elongatus* (**Current IV:** 0.340; **RCP 4.5 IV:** 0.335) and *P. henkelii* (**Current IV:** 0.553; **RCP 8.5 IV:** 0.544). Under RCP 8.5, the most influential variable shaping the distribution of *P. elongatus* was mean temperature of the wettest quarter (BIO8; 0.492). Max

266 temperature of the warmest month (BIO5) constrained the distribution of *P. henkelii* under RCP 4.5
267 (0.414)

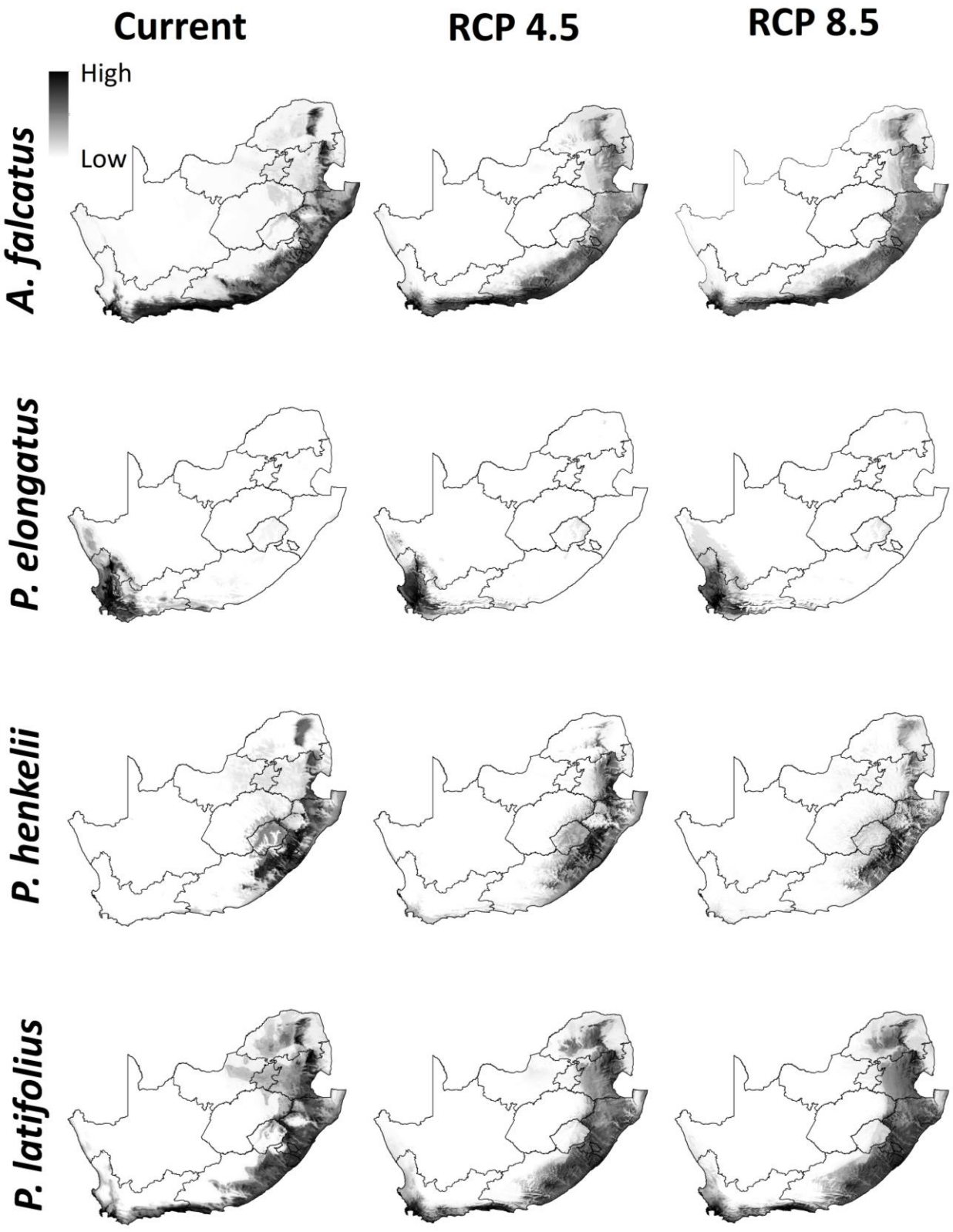
Table 2. Environmental variable importance scores (mean and standard deviation is shown for the three iterations) for *Afrocarpus falcatus, Podocarpus elongatus, P. henkelii* and *P. latifolius* species distribution models under current and future climate emissions scenarios. Variable importance scores range between 0 (low importance) and 1 (high importance). The variables represented in bold were the most important variable for each taxon under current and future conditions.

Species	Emission Scenario	BIO5	BIO7	BIO8	BIO11	BIO16	BIO17	BIO18
A. falcatus	Current	0.084 (0.001)	0.188 (0.002)	0.024 (0.001)	0.157 (0.002)	0.046 (0.001)	**0.455 (0.007)**	0.116 (0.001)
	RCP 4.5	0.056 (0.001)	**0.607 (0.001)**	0.029 (0.001)	0.079 (0.001)	0.037 (0.001)	0.126 (0.002)	0.066 (0.000)
	RCP 8.5	0.029 (0.000)	**0.554 (0.008)**	0.037 (0.001)	0.059 (0.000)	0.122 (0.001)	0.084 (003)	0.115 (0.002)
P. elongatus	Current	0.035 (0.001)	0.045 (0.002)	0.168 (0.006)	0.029 (0.002)	0.121 (0.003)	0.262 (0.015)	**0.340 (0.005)**
	RCP 4.5	0.051 (0.001)	0.100 (0.002)	0.168 (0.003)	0.046 (0.002)	0.178 (0.006)	0.123 (0.005)	**0.335 (0.005)**
	RCP 8.5	0.094 (0.004)	0.154 (0.005)	**0.492 (0.011)**	0.051 (0.001)	0.104 (0.004)	0.043 (0.002)	0.063 (0.003)
P. henkelii	Current	0.095 (0.001)	0.010 (0.001)	0.011 (0.000)	0.040 (0.002)	0.068 (0.001)	0.222 (0.017)	**0.553 (0.017)**
	RCP 4.5	**0.414 (0.008)**	0.184 (0.003	0.122 (0.001)	0.083 (0.002)	0.100 (0.002)	0.059 (0.001)	0.040 (0.001)
	RCP 8.5	0.284 (0.003)	0.080 (0.000)	0.035 (0.001)	0.045 (0.002)	0.057 (0.001)	0.056 (0.006)	**0.544 (0.003)**
P. latifolius	Current	0.254 (0.009)	0.197 (0.004)	0.037 (0.001)	0.054 (0.001)	**0.281 (0.002)**	0.081 (0.001)	0.097 (0.002)
	RCP 4.5	0.078 (0.002)	**0.542 (0.001)**	0.037 (0.001)	0.099 (0.001)	0.173 (0.008)	0.028 (0.000)	0.043 (0.001)
	RCP 8.5	0.052 (0.001)	**0.585 (0.007)**	0.035 (0.001)	0.079 (0.002)	0.191 (0.003)	0.020 (0.000)	0.039 (0.001)

3.2. South African podocarp distribution under climate change

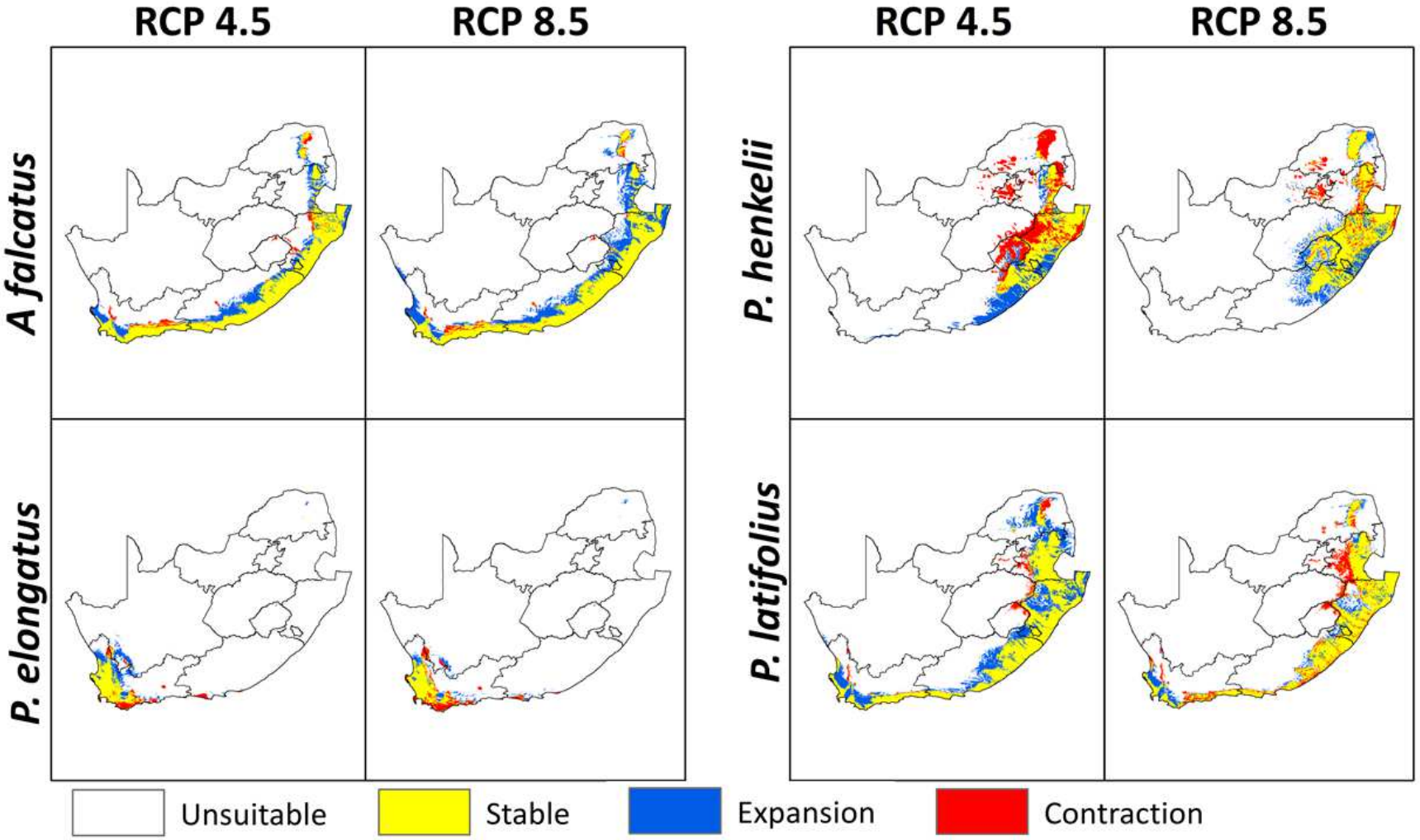
The ensemble SDM predicted high habitat suitability for *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius* in the exterior part of the country, near the coastal limits and are excluded on the interior of the country (Figure 2). All four podocarps had a disjunct distribution of high habitat suitability and were prevalent in high rainfall regions of the country. *Podocarpus latifolius* occupied the largest current and future geographic area followed by *A. falcatus*. *Afrocarpus falcatus* and *P. latifolius* were distributed in the Limpopo, Mpumalanga, KwaZulu-Natal, Eastern Cape, and Western Cape provinces, which span the summer and winter rainfall regions of the country. *Podocarpus elongatus* was restricted to the southern parts of the Western Cape, which is associated with winter rainfall. *Podocarpus henkelii* was constrained to the summer rainfall provinces of Mpumalanga, the midlands of KwaZulu-Natal, and the Eastern Cape, with moderately suitable habitat in the Limpopo province. Although *P. elongatus* and *P. henkelii* had the most restricted distribution, *P. elongatus* had the occupied the smallest geographic area.

Under climate emission scenarios, *A. falcatus* was predicted to expand to higher altitudes into the interior of the country, this was the case for under RCP 4.5 and RCP 8.5 (Figure 3). The southwestern part of the distribution of *P. elongatus* was predicted to expand to higher elevations to track favourable conditions; however, the south-eastern and the northern part of the distribution was predicted to become less suitable under both RCPs. Interestingly, the suitable habitat of *P. henkelii* under current climate was predicted to lose most of its suitable habitat under RCP 4.5 and expanding its habitat to higher altitude in its northern distribution. This was the opposite for *P. latifolius,* where it gained suitable habitat under RCP 4.5 and lost suitable habitat under RCP 8.5. A common finding was that all four podocarp species expanded their habitat by moving to higher altitudes.



296

297 **Figure 2.** Distribution for *Afrocarpus falcatus*, *Podocarpus elongatus, P. henkelii,* and *P. latifolius* in
298 South Africa predicted by using ensemble models based on climatic environmental variables under
299 the current climate and mild (RCP 4.5) and severe (RCP 8.5) climate emission scenarios predicted for
300 2070. Habitat suitability ranges from high (black), moderate (grey) to low (white) suitability.

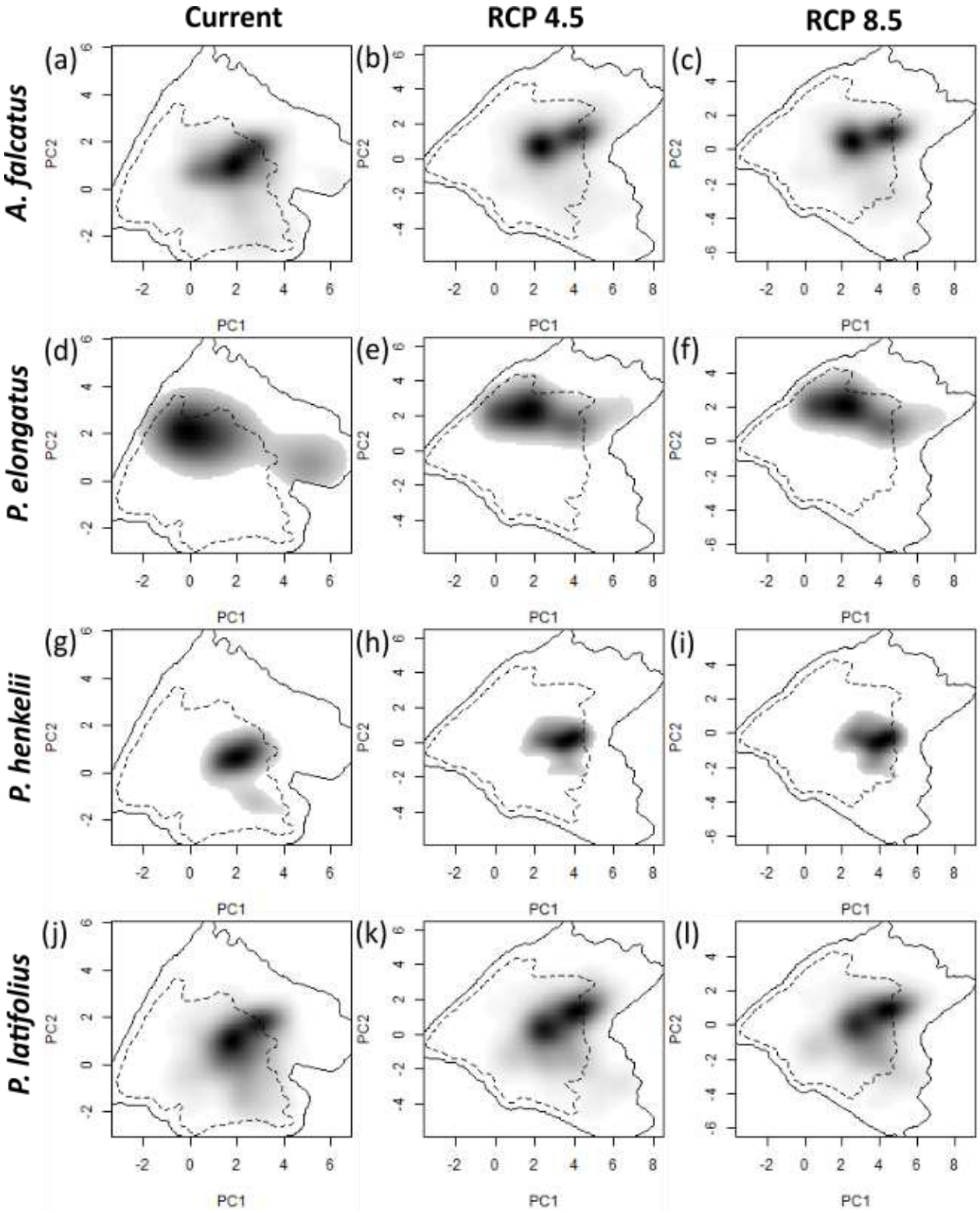


301

302 **Figure 3.** The projected impact of climate change (2070) on the habitat suitability of *Afrocarpus falcatus, Podocarpus latifolius, Podocarpus elongatus* and
303 *Podocarpus henkelii* in South Africa under RCP 4.5 and 8.5 climate emissions scenarios. Yellow represents stability of geographic space, blue represents
304 areas of habitat expansion, and red represents areas of habitat contraction/loss.

3.3. Environmental niche overlap and similarity

The PCAs showed how each podocarp species are distributed along principal climate niche axes under different climatic conditions. *Podocarpus elongatus* occurs over the largest environmental niche, while *P. henkelii* occurs over the smallest environmental niche (Figure 4). The current environmental niches of *A. falcatus, P. elongatus* and *P. henkelii* are predicted to contract in 2070, however the environmental niche of *P. latifolius* is predicted to remain stable under RCP 4.5 and 8.5.



312

313 **Figure 4.** Current and future (RCP 4.5 & RCP 8.5) environmental niches of *Afrocarpus falcatus* (a – c)*,*

314 *Podocarpus elongatus* (d – f)*, P. henkelii* (g – i) and *P. latifolius* (j – l)*.* Darker shading indicates higher

315 densities. The solid line indicates 100% of the available environmental space and the dashed contour

316 lines represent 50% of the most common background space.

3.3.1. Podocarp environmental niche similarity

The environmental niches of all species comparisons were dissimilar under current and future climate scenarios (Table 3; Figure 4).

Table 3. Niche comparisons for *Afrocarpus falcatus, Podocarpus elongatus, P. henkelii* and *P. latifolius*. Niche overlap values (Schoener's *D*) are presented for the comparisons of niche similarity of each species under current and future climate emissions scenarios (RCP 4.5 and RCP 8.5). Significant similarity test *P*-values are in bold.

Species	Similarity value (*D*)		
	Current	RCP 4.5	RCP 8.5
A. falcatus → P. elongatus	0.3267	0.2475	0.1584
A. falcatus ← P. elongatus	0.2871	0.2277	0.1881
A. falcatus → P. henkelii	0.2475	0.2277	0.2574
A. falcatus ← P. henkelii	0.2079	0.1584	0.2376
A. falcatus → P. latifolius	0.1980	0.2475	0.1287
A. falcatus ← P. latifolius	0.2178	0.3564	0.1287
P. elongatus → P. henkelii	0.2277	0.2277	0.1683
P. elongatus ← P. henkelii	0.3168	0.2673	0.2376
P. elongatus → P. latifolius	0.2970	0.3663	0.3960
P. elongatus ← P. latifolius	0.2871	0.4158	0.3960
P. henkelii → P. latifolius	0.2376	0.2673	0.2178
P. henkelii ← P. latifolius	0.2772	0.3762	0.1782

3.3.2. Niche overlap between the current and future environmental niches

The current and future environmental niches of *A. falcatus, P. elongatus* and *P. latifolius* showed very limited overlap (Table 4; Figure 4). Interestingly, *P. henkelii* had the highest environmental niche overlap of the four podocarps with 59.17% and 55.43% overlap between the current–RCP 4.5 and current–RCP 8.5 environmental niches, respectively.

When the overlap between the current and future environmental niches were further broken down, we observed that the current and future environmental niches of all four podocarps was stable (Table 4). *Afrocarpus falcatus* showed greater niche expansion (**Current → RCP 4.5:** 0.35; **Current → RCP 8.5:** 0.39) compared to niche unfilling (**Current → RCP 4.5:** 0.13; **Current → RCP 8.5:** 0.14). A greater extent of niche unfilling was observed for *P. elongatus* and *P. henkelii* in comparison

335 to niche expansion for both niche comparisons (Table 4). Low niche unfilling (**Current → RCP 4.5:**
336 0.08; **Current → RCP 8.5:** 0.08) and expansion (**Current → RCP 4.5:** 0.30; **Current → RCP 8.5:** 0.29)
337 was observed for *P. latifolius* between the current and future environmental niches.

338 **Table 4.** Niche overlap and dynamics between the current and future projected environmental
339 niches of *Afrocarpus falcatus, Podocarpus elongatus, P. henkelii* and *P. latifolius*. Each metric ranges
340 from zero (low) to one (high).

Species	Pairwise comparisons	Niche overlap (*D*)	Expansion	Stability	Unfilling
A. falcatus	Current → RCP 4.5	0.1212	0.3543	0.6456	0.1309
	Current → RCP 8.5	0.1633	0.3869	0.6131	0.1348
P. elongatus	Current → RCP 4.5	0.0759	0.2137	0.7863	0.4936
	Current → RCP 8.5	0.0428	0.3007	0.6993	0.6733
P. henkelii	Current → RCP 4.5	0.5917	0.0240	0.9760	0.3716
	Current → RCP 8.5	0.5543	0.0501	0.9499	0.4335
P. latifolius	Current → RCP 4.5	0.1076	0.3005	0.6995	0.0755
	Current → RCP 8.5	0.2068	0.2884	0.7116	0.0753

341

4. Discussion

This study characterised environmental niches of South African podocarps using ordination techniques to better understand how these species may respond to the changing climate. In addition, we used ensemble SDMs to identify the environmental constraints that shape the current and future geographic distributions of *A. falcatus, P. elongatus, P. henkelii* and *P. latifolius.* We found that the ensemble SDMs accurately predicted the known geographic distributions of each podocarp species, that podocarps were generally limited by rainfall, particularly around the seed germination timeframe, and that there are likely physiological traits and reproductive mechanisms that potentially prevent species from dispersing outside their current distributions.

Identifying environmental variables that shape and maintain species geographic distributions is an essential component of evolution and ecology. Among the seven environmental variables used for these models, total rainfall during the summer and winter months (irrespective of summer/winter rainfall region) was predicted to shape the current and future distribution of podocarps in South Africa. This reliance on rainfall may highlight that podocarps are actually constrained by drought (Brodribb and Hill 1998). Nearly all extant podocarps exhibit low to no drought tolerance (Brodribb and Hill 2004) except for the New Zealand species *P. totara,* which uses drought-avoidance strategies (Innes and Kelly 1992) and *P. macrophyllus* found across China and Japan (He et al. 2020). Consequently, podocarps may be limited to high rainfall areas due to traits that may affect their ability to survive in low rainfall regions. For instance, podocarps have small single-veined leaves that limit hydraulic conductivity (Brodribb et al. 2007) and recalcitrant seeds that become less viable as they lose moisture (Noel and Staden 1976; Dodd, Staden and Smith 1989a; 1989b; Negash 2003). The models indicated that South African podocarps tend to persist in moist forest patches where fires are an important driver of forest distribution yet fires hardly occur in the patches themselves (Geldenhuys 1994; Kellman and Meave 1997). In addition, *P. latifolius* recruitment is significantly reduced under drought and deep shade where seedlings are outcompeted by grasses in the landscape (Adie and Lawes 2009b). Drought and shade are antagonistic selection pressures and together with rainfall appear to constrain podocarp distribution (Chiariello 1984; Givnish 1987; Brodribb andHill 2000; *reviewed by* Fiorucci and Fankhauser 2017; Lusk et al. 2019).

In addition to rainfall, the future distribution of *A. falcatus* and *P. latifolius* was predicted to be limited by temperature annual range (BIO7). This finding suggests that in the future there will be variation in seasonal temperatures where *A. falcatus* and *P. latifolius* occur across the highlands and midlands in the northeastern parts of South Africa compared to the southwestern parts of the

country. In the northeastern parts of South Africa, the models predict that the future daily temperatures fluctuations will be smaller in comparison to present higher daily temperature fluctuations in the southwestern parts of the country. Notably, the future distribution of *P. elongatus* was also constrained by mean temperature during the wettest quarter, which coincides with the winter months for this species as it is currently restricted to winter rainfall areas of the country. Winter rainfall and temperature are particularly important for *P. elongatus* because it produces recalcitrant seeds during the winter months and minimum rainfall and temperature requirements need to be met for *P. elongatus* recruitment and persistence. *Podocarpus henkelii* may be limited to warm high rainfall areas because it has foliar sclereids and broad leaves (Brodribb and Hill 1998; Adie and Lawes 2011; Brodribb 2011). Furthermore, *P. henkelii* produces seeds that are more drought-sensitive than *A. falcatus* seeds (Dodd et al. 1989a; Negash 1992).

The palaeodistribution of podocarps and considering the role of drought on podocarp distribution in South Africa places the current and future distribution of podocarps into context. The earliest podocarp macrofossils are from Gondwana during the Triassic (including Madagascar), with subsequent records from India, Australasia (Hill 1994), Africa, Patagonia (Gnaedinger 2007), and Antarctica during the Jurassic. Throughout the Cretaceous period Podocarps had a prominent distribution in Gondwana, including Patagonia, with most modern podocarp genera appeared during this period. The radiation of podocarp genera during the Cretaceous period was attributed to the onset of wetter and warmer climatic conditions because of the opening of the Southern Ocean. Although podocarps mainly had a Gondwanan distribution, there are some fossil records from Laurasia. Podocarp dispersal into Africa is unknown, however there is evidence of podocarp pollen from the Early Cretaceous. The first remnants of podocarps in Africa were found in East Africa where they dispersed to the West African highlands following global cooling when the Northern Hemisphere ice sheets expanded. Podocarps have been present at low latitudes in elevated areas of Africa during the Cretaceous and throughout the whole of the Cenozoic.

The current and future potential distributions of podocarps obtained from our ensemble SDMs coincide with known geographic ranges (White 1981; Farjon 2001). The broad geographically distributed *P. latifolius* and *A. falcatus* co-occur with *P. elongatus* and *P. henkelii* in their respective geographic ranges, however *P. elongatus* and *P. henkelii* do not co-occur. *Podocarpus latifolius* had the broadest geographic distribution followed by *A. falcatus*. Both *A. falcatus* and *P. latifolius* were predicted to co-occur in the north-eastern part of South Africa, along the southern coast, and through to the southwest of South Africa. This finding coincides with the actual distribution of each species. The geographic range extends across the savanna, grassland, forest, fynbos, and Albany thicket biomes and extends to the Indian Ocean coastal belt. *Afrocarpus falcatus* is the only one of

these four podocarps that persists in the dry forest of the coastal lowlands (Coomes and Bellingham 2011; Adie and Lawes 2011) and this occurrence is likely as a relic from population expansion during the cool and moist conditions of the last glaciation (Finch and Hill 2008; Neumann et al. 2008). *Podocarpus elongatus* was predicted to occupy the smallest geographic area of all the examined podocarp species under current and future climate emissions scenarios. This taxon is presently distributed in the south and southwestern parts of South Africa within the fynbos and succulent karoo biomes. *Podocarpus elongatus* can persist in this fire prone habitat due to its ability to resprout after fire (Midgley et al. 1995). Unlike the other podocarps, *P. elongatus* produces epicormic sprouts that enable tolerance of fire and persistence in the fynbos biome that is prone to fire (Midgley et al. 1995), which makes it better adapted for Mediterranean habitat. *Podocarpus elongatus* may be restricted to its Gondwanan origin and its disjunct distribution a result of retreating to higher elevations to track favourable environmental conditions as rising sea levels during the Last Glacial Maximum lead to loss of coastal habitat (Geldenhuys 1992). *Podocarpus henkelii* current distribution occurs in summer rainfall regions with high rainfall in eastern Limpopo province, midlands of KwaZulu-Natal, and northern Eastern Cape province of South Africa. Under future scenarios, *P. elongatus* may experience a contraction of its geographic distribution under relatively 'mild' climate change scenarios (e.g., RCP 4.5) yet will potentially expand its geographic distribution as temperatures rise (e.g., under RCP 8.5, Figure 2).

The effects of climate change on the geographic distribution of a wide range of tree communities have been reported across the world (Bakkenes et al. 2002; Aitken et al. 2008; Essl et al. 2011; Aguileé et al. 2019; Burley et al. 2019; Kambach et al. 2019; Pavlović et al. 2019; Sedmáková et al. 2019; Fricke et al. 2022). *Podocarpus henkelii* was predicted to occupy the third largest geographic range under future climate emission scenarios (Figure 2). Its geographic range was predicted to contract in higher elevations and expand to lower elevations for both climate change emission scenarios. The southern expansion of its geographic area under both emission scenarios may suggest that the southern parts of South Africa will become hotter under climate change (Collier et al. 2008). Therefore, it is plausible that *P. henkelii* is a thermophilic species and can expand its distribution with increasing temperatures under climate change. This is also evident through the reduced geographic expansion of *P. henkelii* under RCP 8.5 in comparison to the cooler RCP 4.5 (Figure 3). In contrast, under both emission scenarios, *A. falcatus* and *P. latifolius* were predicted to expand to higher altitudes and lower longitudes to track favourable climatic conditions. The dispersal of *A. falcatus* and *P. latifolius* seeds by birds, bats, baboons, and monkeys (Geldenhuys 1993; Negash 2003) will likely enable them to expand to climatically favourable areas faster relative to *P. elongatus* and *P. henkelii.* The past responses of *P. elongatus* and *P. henkelii* to climate change

indicate a tight synchronisation with climate fluctuations, particularly in response to water availability. For *P. latifolius,* recruitment is then less episodic than the other species thus making it less vulnerable to climatic instability. *Podocarpus elongatus* was predicted to lose suitable habitat in its southern distribution under both RCPs and expand northwards, particularly under RCP 4.5. However, shifting to higher elevations and longitudinal shifts seem to be the most common responses to climate change (Pavlović et al. 2019; Sedmáková et al. 2019).

Numerous studies have reported that plant species that occupy a large geographic range also occupy different environmental niches (Cardillo et al. 2018; Early et al. 2019; Kambach et al. 2019). We found that niche divergence was evident for all pairwise comparisons (Table 3). The tendencies toward divergent environmental niches in podocarps cannot be explained by differences in the climate suitability alone. However, this divergence could be explained by differences in seed dispersal, establishment requirements, habitat use, competition and ecophysiological limits. There was no consistent trend in niche conservatism or divergence among the comparisons of current environmental niches and predicted future niches across the podocarp species examined. For example, *P. henkelii* may shift to new geographic areas under climate change/predicted emission scenarios, per niche conservatism, given the high niche overlap value and unfilling value (i.e., the future environmental niche space is available but currently unoccupied). Notably, there may be elevated propagule pressures that ultimately limit the dispersal of *P. henkelii* to sites with suitable environmental conditions, which will result in a reduced realised niche. It is also possible that *P. henkelii* may continue to spread in its geographic range even though the breadth of its environmental niche is predicted to decrease. Relative to the other three podocarps examined, *P. henkelii* had the lowest niche expansion value, which suggests that it will not expand into novel environmental niches when moving southwards geographically under climate change. On the other hand, the current environmental niche of *P. elongatus* diverged slightly from its future environment niche due to low niche overlap from high niche expansion and unfilling (Table 4). This divergence may be attributed to differences in microhabitats and competition. In addition, the current and future environmental niches of *P. latifolius* showed low niche overlap, which was associated with low niche unfilling values. *Podocarpus latifolius* can occur within areas with variable gradients of soil moisture, temperature, rainfall, and altitude along different latitudes and it produces small seeds annually which are dispersed by birds (Geldenhuys 1993; Adie and Lawes 2009b). Moreover, frequent recruitment occurs due to lower seed susceptibility to desiccation and shade tolerant seeds, which facilitates germination and reduces susceptibility to climate change. These characteristics indicate that *P. latifolius* is a vagile species. Despite this, results showed low niche

476 expansion. This may be because *P. latifolius* currently occupies most of the suitable environmental
477 niche available already, and there is no additional niche to expand into.

478 The ability of a species to occupy different environmental niches may have important
479 implications for the understanding of the vulnerability of the species under climate change (Wiens,
480 & Graham, 2005). Previous studies recognised niche shifts in a variety of plant taxa such as *Picea*
481 *sitchensis* (Aguilée et al. 2016), *Agave* spp. (Gómez-Ruiz and Lacher 2019) and *Betula utilis* (Hamid et
482 al. 2019) under climate change, but the causes of these shifts are not well known. However, several
483 studies have shown that some species will not be able to track favourable climate fast enough to
484 escape climate change (Zhu et al. 2012; Cang et al. 2016; Burley et al. 2019). The combination of
485 some niche expansion and unfilling for *A. falcatus* under both RCPs resulted in moderate niche
486 stability under global change. The inability of *A. falcatus* to occupy environmental niches different
487 from those of its current environmental niche may be due to a combination of post dispersal
488 mortality and loss in seed viability after harvesting, coupled with infrequent fruit production
489 (Geldenhuys 1993; Negash 2003). Additionally, *A. falcatus* may be poor at dispersing into new
490 habitats, but once established it is able to persist. Consequently, dispersal may be the main factor
491 that governs whether *A. falcatus* reaches suitable habitats under global change.

492 Overall, we found that podocarp distribution is determined primarily by seasonal drought,
493 likely due to the recalcitrant seeds of podocarps which are produced generally when rainfall is
494 limited. The difference in the distribution of these podocarps underscores the variation of
495 environmental conditions that they are adapted to and may also be a reflection on the differences in
496 their physiology. This is particularly important as the physiological traits of podocarps may limit their
497 distribution across environmental gradients (Brodribb and Hill, 1998, 1999; Brodribb 2011, *in review*
498 Twala et al. 2022). Physiologically oriented distribution models should be useful to predict whether
499 the physiological thresholds of podocarps are the mechanism responsible for podocarp distribution
500 and not their reproductive means. Insights from this study are useful for on-going conservation
501 actions for South African podocarps by directing the re-introduction of these species in suitable
502 habitats and guiding the establishment of effective networks of protected areas for future dispersal
503 events.

10. References

Adie H, Kotze DJ, Lawes MJ (2017). Small fire refugia in the grassy matrix and the persistence of Afrotemperate forest in the Drakensberg mountains. *Scientific Reports*, *7*(1), pp.1-10.

Adie H, Lawes MJ (2009a). Role reversal in the stand dynamics of an angiosperm–conifer forest: colonising angiosperms precede a shade-tolerant conifer in Afrotemperate forest. *Forest Ecology and Management*, *258*(2), 159-168.

Adie H, Lawes MJ (2009b). Explaining conifer dominance in Afrotemperate forests: shade tolerance favours Podocarpus latifolius over angiosperm species. *Forest Ecology and Management*, *259*(2), 176-186.

Adie H, Lawes MJ (2011). Podocarps in Africa: temperate zone relicts or rainforest survivors?. *Smithsonian Contributions to Botany*, *95*, pp.79-100.

Adie H, Lawes MJ (2011). Podocarps in Africa: temperate zone relicts or rainforest survivors?. *Smithsonian Contributions to Botany*, *95*, 79-100.

Aguilée R, Raoul G, Rousset F, Ronce O (2016). Pollen dispersal slows geographical range shift and accelerates ecological niche shift under climate change. *Proceedings of the National Academy of Sciences*, *113*(39), E5741-E5748.

Aitken SN, Yeama S, Holliday JA, Wang T, Curtis-McLane S (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, *1*(1), 95-111.

Allouche O, Tsoar A, Kadmon R (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology*, *43*(6), 1223-1232.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, *8*(4), 390-407.

Bergin DO (2000). Current knowledge relevant to management of Podocarpus totara for timber. *New Zealand Journal of Botany*, *38*(3), 343-359.

Biffin E, Brodribb TJ, Hill RS, Thomas P, Lowe AJ (2012). Leaf evolution in Southern Hemisphere conifers tracks the angiosperm ecological radiation. *Proceedings of the Royal Society B*, 279 (1727), 341–348.

Boria RA, Olson LE, Goodman SM, Anderson RP (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, *275*, 73-77.

Brodribb T, Hill RS (2000). Increases in water potential gradient reduce xylem conductivity in whole plants. Evidence from a low-pressure conductivity method. *Plant Physiology*, *123*(3), 1021-1028.

Brodribb T, Hill RS (2004). The rise and fall of the Podocarpaceae in Australia—a physiological explanation. In *The evolution of plant physiology* (pp. 381-399). Academic Press.

Brodribb TJ (2011). A Functional Analysis of Podocarp Ecology. In *Ecology of the Podocarpaceae in Tropical Forests,* Turner BL, Cernusak LA, eds., pp. 165‑173. SmithsonianContributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.

Brodribb TJ, Feild TS, Jordan, GJ (2007). Leaf maximum photosynthetic rate and venationare linked by hydraulics. *Plant Physiology*, *144*(4), 1890-1898.

Brodribb TJ, Hill RS (1998). The photosynthetic drought physiology of a diverse group of southern hemisphere conifer species is correlated with minimum seasonal rainfall. *Functional Ecology*, *12*(3), 465-471.

Brodribb TJ, Hill RS (1999). The importance of xylem constraints in the distribution of conifer species. *New Phytologist*, *143*(2), 365-372.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M-F, Randin C, Zimmermann NE, Graham CH, Guisan A (2012). Measuring ecological niche

overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*(4), 481-497.
Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, *10*(8), 701-709.
Burley H, Beaumont LJ, Ossola A, Baumgartner JB, Gallagher R, Laffan S, Esperon Rodriguez M, Manea A, Leishman MR (2019). Substantial declines in urban tree habitat predicted under climate change. *Science of the Total Environment*, *685*, 451-462.
Cang, F. A., Wilson, A. A., & Wiens, J. J. (2016). Climate change is projected to outpace rates of niche change in grasses. *Biology Letters*, *12*(9), 20160368.
Cardillo, M. (2011). Phylogenetic structure of mammal assemblages at large geographical scales: linking phylogenetic community ecology with macroecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1577), 2545-2553.
Cardillo, M., Dinnage, R., & McAlister, W. (2019). The relationship between environmental niche breadth and geographic range size across plant species. *Journal of Biogeography*, *46*(1), 97-109.
Chiariello N (1984). Leaf energy balance in the wet lowland tropics. In *Physiological Ecology of Plants of the Wet Tropics*. Eds. E. Medina, H.A. Mooney and C. Vázquez-Yánes. Proc. Int. Symp. Tasks for Vegetation Science 12. Dr. W. Junk Publishers, The Hague, pp 85 - 98.
Christenhusz MJ, Byng JW (2016). The number of known plants species in the world and its annual increase. *Phytotaxa* 261, 201–217.
Collier P, Conwa G, Venables T (2008). Climate change and Africa. *Oxford Review of Economic Policy*, *24*(2), 337-353.
Contreras DL, Duijnstee IAP, Ranks S, Marshall CR, Looy CV (2017). Evolution of dispersal strategies in conifers: Functional divergence and convergence in the morphology of diaspores. *Perspective in Plant Ecology, Evolution and Systematics*, 24, 93–117.
Coomes DA, Bellingham PJ (2011). Temperate and tropical podocarps: how ecologically alike are they?. *Smithsonian Contributions to Botany*.
Datta A, Schweiger O, Kühn I (2019). Niche expansion of the invasive plant species *Ageratina adenophora* despite evolutionary constraints. *Journal of Biogeography*, *46*(7), 1306-1315.
Di Cola V, Broennimann O, Petitpierre B, Breiner FT, d'Amen M, Randin C, Engler R, Pottier J, Pio D, \ Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*(6), 774-787.
Dodd MC, Staden JV, Smith MT (1989a). Seed development in *Podocarpus henkelii*: an ultrastructural and biochemical study. *Annals of Botany*, *64*(3), 297-310.
Dodd MC, Staden JV, Smith MT (1989b). Seed germination in *Podocarpus henkelii*: an ultrastructural and biochemical study. *Annals of Botany*, *64*(5), 569-579.
Elith J, Graham CH, Anderson RP, Dudı´k M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcCM, Townsend Peterson A, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29(2):129–151
Elith J, Kearney M, Phillips S (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330-342.
Elith J, Leathwick JR (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of Ecology, Evolution, and Systematics*, *40*, 677-697.
Essl F, Dullinger S, Plutzar C, Willner W, Rabitsch W (2011). Imprints of glacial history and current environment on correlations between endemic plant and invertebrate species richness. *Journal of Biogeography*, *38*(3), 604-614.
Farjon A (2001). *World Checklist and Bibliography of Conifers*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

Farjon A (2018). The Kew review: conifers of the world. Kew Bull. 73, 8.
Finch JM, Hill TR (2008). A late Quaternary pollen sequence from Mfabeni Peatland, South Africa: Reconstructing forest history in Maputaland. *Quaternary Research*, *70*(3), 442-450.
Fiorucci AS, Fankhauser C (2017). Plant strategies for enhancing access to sunlight. *Current Biology*, *27*(17), R931-R940.
Fricke EC, Ordonez A, Rogers HS, Svenning JC (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, *375*(6577), 210-214.
Geldenhuys CJ (1993). Reproductive biology and population structures of *Podocarpus falcatus* and *P. latifolius* in southern Cape forests. *Botanical Journal of the Linnean Society*, *112*(1), 59-74.
Geldenhuys CJ (1994). Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. *Journal of Biogeography*, 49-62.
Givnish TJ (1987). Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist*, *106*, 131-160.
Glennon KL, Ritchie ME, Segraves KA (2014). Evidence for shared broad-scale climatic niches of diploid and polyploid plants. *Ecology Letters*, *17*(5), 574-582.
Gnaedinger S (2007). Podocarpaceae woods (Coniferales) from middle Jurassic La Matilde formation, Santa Cruz province, Argentina. *Review of Palaeobotany and Palynology*, *147*(1-4), 77-93.
Gómez-Ruiz EP, Lacher Jr TE (2019). Climate change, range shifts, and the disruption of a pollinator plant complex. *Scientific Reports*, *9*(1), 1-10.
Government Gazette (2016). Notice of the list of protected tree species under the national forests act, 1998 (act no. 84 of 1998).
Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014). Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution*, *29*(5), 260-269.
Guisan A, Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, *8*(9), 993-1009.
Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDondald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, *16*(12), 1424-1435.
Gutiérrez EE, Boria RA, Anderson RP (2014). Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums. *Ecography*, *37*(8), 741-753.
Hamid M, Khuroo AA, Charles B, Ahmad R, Singh CP, Aravind NA (2019). Impact of climate change on the distribution range and niche dynamics of Himalayan birch, a typical treeline species in Himalayas. *Biodiversity and Conservation*, *28*(8), 2345-2370.
Hanley JA, McNeil BJ (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, *143*(1), 29-36.
He C, Zhao Y, Zhang J, Gao J (2020). Chitosan Oligosaccharide Addition to Buddhist Pine (*Podocarpus macrophyllus* (Thunb) Sweet) under Drought: Reponses in Ecophysiology and δ13C Abundance. *Forests*, *11*(5), 526.
Hill RS, Brodribb T (1999). Southern conifers in time and space. *Australian Journal of Botany* 47, 639–696.
Innes KP, Kelly D (1992). Water potentials in native woody vegetation during and after a drought in Canterbury. *New Zealand Journal of Botany*, *30*(1), 81-94.
Jentsch H, Bobrowski M, Weidinger W (2021). ClimDatDownloadR: Downloads Climate Data from Chelsa and WorldClim. R package version 0.1.5.
Kambach S, Lenoir J, Decocq G, Welk E, Seidler G, Dullinger S, Gégout J-C, Guisan A, Pauli H, Svenning J-C, Vittoz P, Wohlgemuth T, Zimmermann NE, Bruelheide H (2019). Of niches and distributions: range size increases with niche breadth both globally and regionally but regional estimates poorly relate to global estimates. *Ecography*, *42*(3), 467-477.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), pp.1-20.

Kellman M, Meave J (1997). Fire in the tropical gallery forests of Belize. *Journal of Biogeography*, *24*(1), 23-34.

Krassilov VA (1974). *Podocarpus* from the Upper Cretaceous of Eastern Asia and Its Bearing on the Theory of Conifer Evolution. *Palaeontology*, 17: 365‑370.

Legesse N (1992). In vitro methods for the rapid germination of seeds of *Podocarpus falcatus*. *Sinet*, *15*(2), 85-97.

Leslie AB, Beaulieu JM, Rai HS, Crane PR, Donoghue MJ, Mathews S (2012). Hemisphere scale differences in conifer evolutionary dynamics. Proc. Natl. Acad. Sci. USA 109 (40), 16217–16221.

Lusk CH, Grierson ER, Laughlin DC (2019). Large leaves in warm, moist environments confer an advantage in seedling light interception efficiency. *New Phytologist*, *223*(3), 1319-1327.

Meinshausen M, Smith SJ, Calvin K, Daniel JS, Kainuma ML, Lamarque JF, Matsumoto S, Montzka SA, Raper SCB, Riahi K, Thomson A, Velders GJM, Van Vuuren DPP (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, *109*(1), 213-241.

Midgley JJ, Bond WJ, Geldenhuys CJ (1995). The Ecology of the Southern African Conifers. In *Ecology of the Southern Conifers*, Enright NJ, Hill RS, eds., pp. 64-80. Melbourne University Press, Carlton, Australia.

Migliore J, Lézine AM, Hardy OJ (2020). The recent colonization history of the most widespread *Podocarpus* tree species in Afromontane forests. *Annals of Botany*, *126*(1), 73-83.

Migliore J, Lézine AM, Veuille M, Achoundong G, Tchiengué B, Boom AF, Monthe FK, Bouka GUD, Omondi SF, Wagura L, Gonçalves FMP, Stévart T, Farminhão JNM, Hardy OJ (2022). Origin, Persistence, and Vulnerability to Climate Changes of *Podocarpus* Populations in Central African Mountains. *Forests*, *13*(2), 208.

Molloy BPJ (1995). Manoao (Podocarpaceae), a new monotypic conifer genus endemic to New Zealand. *New Zealand Journal of Botany*, *33*(2), 183-201.

Morales CL, Arbetman MP, Cameron, SA, Aizen MA (2013). Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*, *11*(10), 529-534.

Moran EV (2020). Simulating the effects of local adaptation and life history on the ability of plants to track climate shifts. *AoB Plants*, *12*(1), plaa008.

Neale DB, Wheeler NC (2019). In: The Conifers: Genomes, Variation and Evolution. Springer International Publishing, Cham, pp. 1–21. https://doi.org/10.1007/978-3- 319-46807-5_1.

Negash L (1995). *Indigenous trees of Ethiopia. Biology, uses and propagation techniques. Repro.* SLU, Umeå, Sweden.

Negash L (2003). In situ fertility decline and provenance differences in the East African Yellow Wood (Podocarpus falcatus) measured through in vitro seed germination. *Forest Ecology and Management*, *174*(1-3), 127-138.

Neumann FH, Stager JC, Scott L, Venter HJ, Weyhenmeyer C (2008). Holocene vegetation and climate records from lake Sibaya, KwaZulu-Natal (South Africa). *Review of Palaeobotany and Palynology*, *152*(3-4), 113-128.

Noel ARA, Van Staden J (1976). Seed coat structure and germination in *Podocarpus henkelii*. *Zeitschrift für Pflanzenphysiologie*, *77*(2), 174-186.

Pang SE, De Alban JDT, Webb EL (2021). Effects of climate change and land cover on the distributions of a critical tree family in the Philippines. *Scientific Reports*, *11*(1), 1-13.

Pavlović L, Stojanović D, Mladenović E, Lakićević M, Orlović S (2019). Potential elevation shift of the European beech stands (*Fagus sylvatica* L.) in Serbia. *Frontiers in Plant Science*, *10*, p.849.

Peterson AT (2011). Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography*, *38*(5), 817-827.

706 Peterson AT, Soberón, J, Sánchez-Cordero V (1999). Conservatism of ecological niches in
707 evolutionary time. *Science*, *285*(5431), 1265-1267.
708 Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan, A (2012). Climatic niche shifts
709 are rare among terrestrial plant invaders. *Science*, *335*(6074), 1344-1348.
710 Pigot AL, Tobias JA (2013). Species interactions constrain geographic range expansion over
711 evolutionary time. *Ecology Letters*, *16*(3), 330-338.
712 Porfirio LL, Harris RM, Lefroy EC, Hugh S, Gould SF, Lee G, Bindoff, NL, Mackey B (2014). Improving
713 the use of species distribution models in conservation planning and management under
714 climate change. *PLoS One*, *9*(11), e113749.
715 Quiroga MP, Premoli AC (2007). Genetic patterns in *Podocarpus parlatorei* reveal the long-term
716 persistence of cold-tolerant elements in the southern Yungas. *Journal of*
717 *Biogeography*, *34*(3), 447-455.
718 Rödder D, Engler JO (2011). Quantitative metrics of overlaps in Grinnellian niches: advances and
719 possible drawbacks. *Global Ecology and Biogeography*, *20*(6), 915-927.
720 Schoener TW (1968). The Anolis lizards of Bimini: resource partitioning in a complex
721 fauna. *Ecology*, *49*(4), 704-726.
722 Sedmáková D, Sedmák R, Bosela M, Ježík M, Blaženec M, Hlásny T, Marušák R (2019). Growth
723 climate responses indicate shifts in the competitive ability of European beech and Norway
724 spruce under recent climate warming in East-Central Europe. *Dendrochronologia*, *54*, 37-48.
725 Soberón J (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology*
726 *Letters*, *10*(12), 1115-1123.
727 Synes NW, Osborne PE (2011). Choice of predictor variables as a source of uncertainty incontinental-
728 scale species distribution modelling under climate change. *Global Ecology and*
729 *Biogeography*, *20*(6), 904-914.
730 Warren DL, Glor RE, Turelli M (2008). Environmental niche equivalency versus conservatism:
731 quantitative approaches to niche evolution. *Evolution: International Journal of Organic*
732 *Evolution*, *62*(11), 2868-2883.
733 White F (1981). The history of the Afromontane archipelago and the scientific need for its
734 conservation. *African Journal of Ecology, 19*(1-2), 33-54.
735 Wiens JJ (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of
736 species. *Evolution*, *58*(1), 193-197.
737 Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI,Davies TJ, Grytnes
738 J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010). Niche conservatism
739 as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*(10),
740 1310 - 1324
741 Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law
742 EA, Leishman MR, Niinemets Ü, Reich PB, Sack L, Villar R, Wang H, Wilf P (2017). Global
743 climatic drivers of leaf size. *Science*, *357*(6354), 917-921.
744 Yeager TH, Johnson CR (1985). Response of *Podocarpus macrophyllus* to Rock Phosphate and
745 Mycorrhizae. *Journal of Environmental Horticulture*, *3*(4), 168-171.
746 Zhu K, Woodall CW, Clark JS (2012). Failure to migrate: lack of tree range expansion in response to
747 climate change. *Global Change Biology*, *18*(3), 1042-1052.
748 Zimmermann NE (2006). Novel methods improve prediction of species' distributions from
749 occurrence data. *Ecography*, *29*(2), 129-151.

Statements & Declarations

Funding

This research was funded by the National Research Foundation grant to J. T. Fisher (Grant No: 117983), by a National Research Foundation Innovation Scholarship to T. C. Twala (Grant: 117767), and by a Friedel Sellschop Award to K. L. Glennon.

Conflict of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Author Contribution Statement

TCT – Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing – original draft, writing – review & editing.

JTF – Conceptualization, funding acquisition, resources, software, supervision, validation, writing – reviewing & editing.

KLG – Conceptualization, funding acquisition, methodology, resources, supervision, validation, writing – reviewing & editing.

Data Availability

The datasets generated during and/or analysed during the current study are available in the Open Society Foundation repository, DOI 10.17605/OSF.IO/RNG5K (https://osf.io/rng5k/).