



Habitat preference differentiates the Holocene range dynamics but not barrier effects on two sympatric, congeneric trees (*Tristaniopsis*, Myrtaceae)

Monica Fahey^{1,2} · Maurizio Rossetto¹ · Peter D. Wilson¹ · Simon Y. W. Ho^{1,2}

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Abstract

Niche partitioning can lead to differences in the range dynamics of plant species through its impacts on habitat availability, dispersal, or selection for traits that affect colonization and persistence. We investigated whether niche partitioning into upland and riparian habitats differentiates the range dynamics of two closely related and sympatric eastern Australian trees: the mountain water gum (*Tristaniopsis collina*) and the water gum (*T. laurina*). Using genomic data from SNP genotyping of 480 samples, we assessed the impact of biogeographic barriers and tested for signals of range expansion. Circuit theory was used to model isolation-by-resistance across three palaeo-environment scenarios: the Last Glacial Maximum, the Holocene Climate Optimum and present-day (1950–2014). Both trees showed similar genetic structure across historically dry barriers, despite evidence of significant environmental niche differentiation and different post-glacial habitat shifts. *Tristaniopsis collina* exhibits the signature of serial founder effects consistent with recent or rapid range expansion, whilst *T. laurina* has genetic patterns consistent with long-term persistence in geographically isolated populations despite occupying a broader bioclimatic niche. We found the minor influence of isolation-by-resistance on both species, though other unknown factors appear to shape genetic variation. We postulate that specialized recruitment traits (adapted to flood-disturbance regimes) rather than habitat availability limited post-glacial range expansion in *T. laurina*. Our findings indicate that niche breadth does not always facilitate range expansion through colonization and migration across barriers, though it can promote long-term persistence in situ.

Introduction

Range dynamics describe the changing geographic distributions of species in response to environmental shifts over time. The factors that govern climate-driven range shifts are key to understanding the evolutionary history of species and their projected vulnerability to future climate threats. Among plant species, range dynamics are broadly

characterized by the ability to track suitable habitat through propagule dispersal and establishment ('dispersal potential') or to withstand environmental change in situ ('persistence potential'). Habitat specialization is expected to differentiate these processes among species if they differ in eco-physiological tolerances ('environmental niche breadth'; Ackerly 2003; Chase and Leibold 2003) or habitat connectivity across the landscape. However, these distinctions might be cryptic among sympatric species, as their present-day distributions could be the outcome of either recent range expansions or long-term local persistence. Furthermore, since the magnitude of climate change varies geographically, populations located in different parts of a species' range can also be expected to respond differently (Sork et al. 2010). In this context, we seek to investigate whether habitat preference differentiates the range dynamics of closely related and sympatric species; and the extent to which this varies across their range.

The latitudinal climate gradient of mainland eastern Australia shifts from temperate to subtropical systems,

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✉ Monica Fahey
Monica.Fahey@rbgsyd.nsw.gov.au

¹ National Herbarium of New South Wales, Royal Botanic Gardens & Domain Trust, Sydney, Australia

² School of Life and Environmental Sciences, University of Sydney, Sydney, Australia

making this an ideal region for investigating geographic patterns of climate-driven range shifts. The pollen fossil record indicates that substantial vegetation shifts occurred following the end of the Last Glacial Maximum (LGM, 21,000–17,000 years ago), yet there is a paucity of data on the widely distributed mesic flora of the region (although see Mellick et al. 2012). Glaciation during the LGM was less significant in eastern Australia than in the Northern Hemisphere, though conditions were much colder and drier than at present and the period was marked by an elevated fire frequency and intensity (Kershaw et al. 2007). In addition, several large, low-lying river systems formed dry habitat barriers for moisture-dependent species during glacial periods (Thom et al. 1994). Meanwhile, the onset of the Holocene about 12,000 years ago saw a dramatic rise in global temperatures and precipitation, which peaked around 6000 years ago during the Holocene Climactic Optimum (HCO). The impact of LGM habitat barriers and the rate of post-LGM range expansion appears to vary among ecologically-differentiated species (Mellick et al. 2013a, 2014; Rossetto et al. 2015a), though the roles of different factors remain unclear.

A major gap in our understanding of climate-driven range shifts is the relative importance of dispersal versus persistence in available habitat. A number of studies have demonstrated that dispersal mechanism and habitat preference affect restrictions across biogeographic barriers

(Rossetto et al. 2007, 2009, 2015a, b; Milner et al. 2012; Worth et al. 2017), yet the ecological factors that determine survival in refugia are less clear. For instance, chloroplast phylogeographies of cool temperate trees indicate long-term persistence and local re-expansion from multiple glacial refugia across southeast Australia, regardless of dispersal mechanism (Clark and Carbone 2008; Worth et al. 2009, 2010; Nevill et al. 2010). On the other hand, species that are less cold-tolerant but wind-dispersed appear to have relied on long-distance dispersal from relatively few refugia (Worth et al. 2011), suggesting the role of bioclimatic tolerances. We explore these questions with tests of Holocene range expansion in two sympatric trees thought to differ in their potential for persistence and post-LGM dispersal.

Tristaniopsis collina Peter G. Wilson and J. T. Waterh ('mountain water gum') and *Tristaniopsis laurina* Peter G. Wilson and J. T. Waterh ('water gum') are medium-sized trees of the Myrtaceae family and are relatively widespread through the coast and ranges of eastern New South Wales (NSW; Fig. 1a). The species belong to sister clades in a monophyletic Australian lineage of *Tristaniopsis* but show marked ecological differences. While *Tristaniopsis collina* prefers habitats at elevation and typically occurs on rocky hillslopes or escarpment edges, *T. laurina* is restricted to rocky watercourses (Wilson 1991). The upslope and riparian habitats of the two species are thought to have been differently affected by climatic change over time and thus

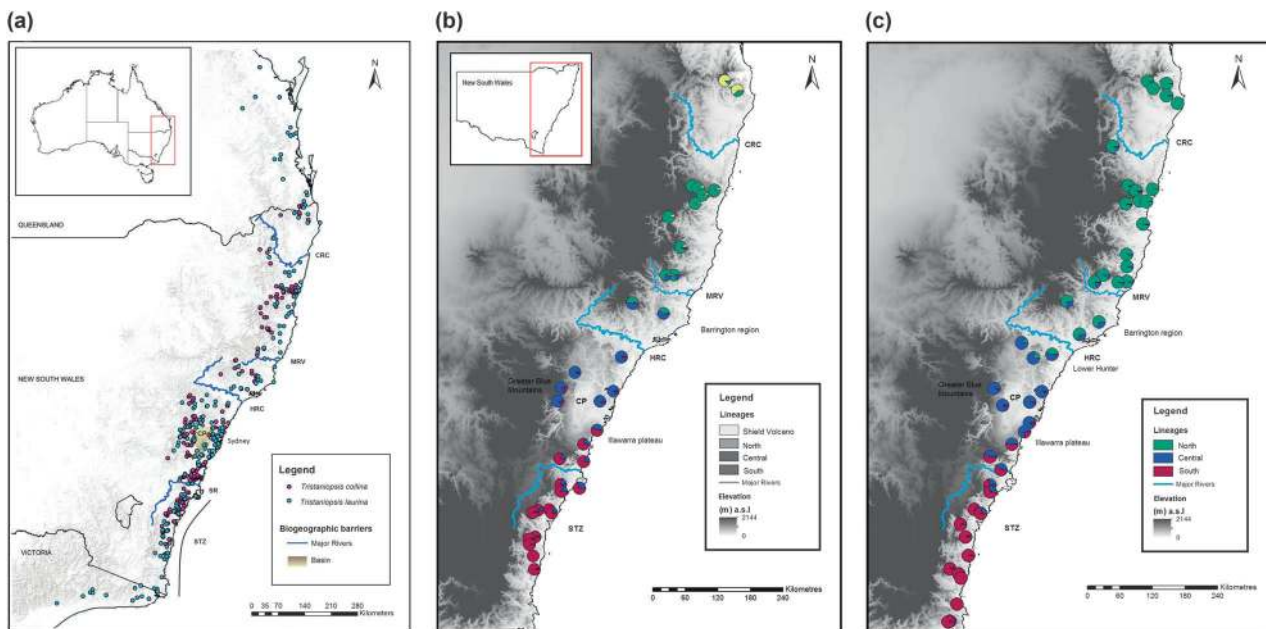


Fig. 1 **a** The occurrence records of *Tristaniopsis collina* and *T. laurina* in eastern Australia, and their distributional extent indicated by the red box (inset map). Areas of significance are shown, including a number of known biogeographic barriers: the Clarence River Corridor (CRC), Manning River Valley (MRV), Hunter River Corridor (HRC), Cumberland Plain (CP), Shoalhaven River (SR), and Southern Transition

Zone (STZ). **b** The study area in eastern New South Wales is indicated by the red box. Sample sites ($n = 6$) and their average population assignment proportions are represented as pie charts. Each colour represents a lineage identified by sNMF, assuming $K = 4$ for *T. collina* and **c** assuming $K = 3$ for *T. laurina*

differentiate their persistence potential. Specifically, sites above 1000 m were too cold for woody species during the LGM (Sweller and Martin 2001; Hesse et al. 2003) and would have forced upland trees like *T. collina* into local extinction or to retreat to lower clines. Meanwhile, lower evapotranspiration rates at riparian sites within montane gullies are hypothesized to have provided microrefugia for lowland trees in periods of drought (Aide and Rivera 1998; de Lafontaine et al. 2014) and potentially enabled greater in situ persistence for *T. laurina*. To test this hypothesis, we first determine the degree of bioclimatic differentiation between the species and then assess their respective Holocene habitat availabilities with palaeo-environment models.

Habitat connectivity is also an important factor in post-LGM dispersal (Sork et al. 2010) and is likely to have differentiated the study species. Riparian habitats are particularly distinct from other habitat types because their linear distribution patterns can function to rapidly disperse propagules across the landscape (Werth and Scheidegger 2014). However, hydrochory (propagule dispersal via water) can only transport genes downstream and is subject to the landscape terrain. This raises the question of whether or not hydrochory facilitates long-distance dispersal of *T. laurina* propagules within catchments (Nilsson et al. 2010). The impact of stream connectivity on population genetic structure has been demonstrated in a number of riparian plants (Wei et al. 2013; Werth and Scheidegger 2014). Yet there are few, if any studies that have evaluated the range dynamics of riparian versus upslope trees in a comparative framework.

Aside from their ecological differentiation, we chose to focus on *Tristaniopsis* species because, in addition to their geographically overlapping distributions (~1200 km), they frequently co-occur in the same community, sometimes only metres apart (M. Fahey, *pers. obs*). The two species also share numerous phenological traits, including similar flowering times and reproductive morphology, though there is no evidence that they hybridize (Wilson and Waterhouse 1982). Aside from minor differences in petal size and stamen abundance, an overall similarity in floral morphology suggests that the species receive similar floral visitors and pollen dispersers (Thomson et al. 2000; Castellanos et al. 2003; Rosas-Guerrero et al. 2011; Wilson et al. 2017). Both possess woody, capsular, 3-valved fruits that contain 30–40 small, terminally winged seeds thought to be mostly gravity-dispersed (Williams and Adam 2010). In this regard, the two species can be expected to encounter similar biogeographic influences and to have equal potential for pollen dispersal.

In this study, we evaluate the population genetic structure of *T. collina* and *T. laurina* with single-nucleotide polymorphisms (SNPs) and construct palaeo-environment models to investigate their range dynamics in eastern NSW,

Australia. Here we use a relatively novel demographic model to test for the signature of serial founder spatial expansions within species (Peter and Slatkin 2013, 2015). We also calculate resistance surfaces based on circuit theory (Shah and McRae 2008) to model the change in habitat connectivity for each species during the Holocene, which is poorly tested in tree species (although see Ortego et al. 2015). Specifically, we tested the following hypotheses:

(1) There is environmental differentiation between the upslope and riparian habitats of *T. collina* and *T. laurina*, and these were differently affected by Holocene climatic fluctuations.

(2) The influence of biogeographic barriers varies between species, due to differences in habitat availability and/or the relative efficacy of hydrochory versus gravity dispersal.

(3) Environmental niche partitioning differentiates the two study species in their potential for range expansion and persistence in refugia.

(4) Within each species, range dynamics vary across the study area, owing to spatial variation in landscape barriers and a latitudinal climate gradient.

Materials and methods

Study system and sampling strategy

We collected foliage samples from the core range of *Tristaniopsis collina* and *T. laurina* in NSW (Fig. 1). This included lowland coastal and adjacent upland locations, and sites separated by putative biogeographic barriers. The Clarence River Corridor in northern NSW is largest coastal catchment in the state, and vicariance across its broad floodplain has been demonstrated in various rainforest trees (Mellick et al. 2011; Heslewood et al. 2014; Rossetto et al. 2015b). The Hunter River Corridor in central NSW is the oldest known barrier in eastern Australia (Chapple et al. 2011) and disrupts latitudinal gene flow in several plant and animal species (Playford et al. 1993; Worth et al. 2009; Chapple et al. 2011; Milner et al. 2012; Heslewood et al. 2014).

Also influential are the climatic gradients of the ‘Southern Transition Zone’ (Milner et al. 2012), which extends southwards from the Shoalhaven River to Victoria. This region has had a complex history of genetic breaks along the coastal escarpment as lowland and upland populations were differently affected by glaciation (Chapple et al. 2011; Milner et al. 2012). The impact of the Southern Transition Zone on the genetic structure of different species is hypothesized to vary with their physiological tolerances (Milner et al. 2012).

We selected the most proximate sites possible between species, so as to have a uniform and comparable sampling

design. We took genetic material from six individuals separated by a minimum distance of 30 m from each locality, which included a total of 34 populations of *T. collina* and 46 populations of *T. laurina* (Supplementary Table S1). All collections were made during April–May 2015 and February–May 2016. Based on our previous analyses of SNP data with DArTseq, we found that six samples per population is sufficient to capture site-level genetic variation (Rossetto et al. 2018).

Quantification of environmental niche breadth and differentiation

In order to assess whether habitat preference varies the range dynamics of *T. collina* and *T. laurina*, we first sought to determine the degree of environmental differentiation between them. We quantified environmental niche separation between the study species from environmental data recorded at their georeferenced occurrence records. The occurrence data were derived from our sample sites, in addition to records obtained from Australia's Virtual Herbarium (<http://avh.chah.org.au>). The occurrence data were filtered to remove records older than 1970 or with spatial uncertainty >1 km. To limit spatial bias, we only included one record per 5 km radius. The final data set consisted of 112 occurrence points for *T. collina* and 118 occurrence points for *T. laurina*.

To reconstruct the environmental background of the study area, we obtained 23 bioclimatic and seven geomorphological variables at a spatial resolution of 36 s (c. 1 km) from eMAST (Xu and Hutchinson 2013). This included the 19 BioClim variables, Mean Monthly Evaporation, Minimum Monthly Evaporation, Maximum Monthly Evaporation, and Evaporation Seasonality. The geomorphological variables included Slope, Aspect, Topographic Wetness Index, Topographic Position Index, Clay %, Sand %, and Silt %. The spatial extent of the study area was bounded to include a 20 km buffer zone around the northern- and southernmost occurrences of *T. laurina* (−24.8° S, −37.8° S, 147° E, 154° E). We quantified niche overlap between *T. collina* and *T. laurina* and the niche breadth of each species in multidimensional environmental space, using a principal components analysis (PCA) method developed by Broennimann et al. (2012) and implemented in the R package Ecospat (Broennimann et al. 2012; Di Cola et al. 2017). This method estimates the niche breadth of each species from the first two axes of a PCA of the 30 predictor variables and visualizes niche space with boxplots for each axis. Niche overlap between species was estimated with Schoener's *D* similarity index, ranging between 0 (no overlap) and 1 (complete overlap; Schoener 1970). We also conducted a niche equivalency test to determine whether the niches of two entities from distinct geographical ranges are equivalent (*D*).

One limitation with our models is that the environmental layers could not be downscaled to the resolution of hydrological datasets (25 m), and so we could not accurately model the riparian microclimate. The spatial resolution is also potentially too coarse to distinguish between the localized changes in Topographic Wetness Index and slope that are believed to differentiate the species. While this would lead to an over-estimated niche breadth for *T. laurina*, the bioclimatic variables are still useful for inferring broader biogeographic trends across the landscape and between species.

Genomic methods

DNA extraction from leaf samples and SNP genotyping using DArTseq technology (Sansaloni et al. 2011) was undertaken at Diversity Arrays Technology Pty Ltd (Canberra, Australia). We evaluated the impact of data quality on downstream diversity analyses through the comparison of SNP data sets filtered according to different quality thresholds: reproducibility average (proportion of technical replicates for which the marker score is consistent) and call rate (proportion of individuals with non-missing scores). We selected markers with a reproducibility average of 0.96 and call rate ≥ 0.95 , which yielded a final data set of 8215 SNPs for 204 samples of *T. collina* and 10,883 SNPs for 276 samples of *T. laurina*.

Assessment of genotypic diversity and population structure

We sought to assess whether population structure within the study species is characterized by divergence across ancient habitat barriers. First, we used the individual ancestry and population clustering algorithm implemented by the R package sNMF (Frichot et al. 2014) to identify putative ancestral lineages. In a procedure similar to that implemented by the widely used program STRUCTURE (Pritchard et al. 2000), ancestry coefficients (*K*) were estimated by running 10 iterations each of *K* = 2 to *K* = 10, and the best-supported *K* was assessed with a cross-entropy criterion (see Frichot et al. 2014). The `find.clusters` and `dapc` function in `adegenet` was used to verify the results of sNMF. This procedure transforms data using a PCA and runs successive *k*-means with an increasing number of clusters (*k*), before performing a linear discriminant analysis on the principal components to assign individuals to clusters (Jombart et al. 2010). For each model, a statistical measure of goodness of fit is computed with the Bayesian information criterion to identify the optimal *k*. Clustering methods have been critiqued for assigning discrete clusters to species potentially characterized by continuous patterns of genetic differentiation (Lawson et al. 2018). Therefore, we ran a

PCA of the individual pairwise genetic distance matrix using the R package *adegenet* 2.0.0 (Jombart 2008; Jombart and Ahmed 2011). Ordination of the first two principal components was used to visualize genetic similarity among samples and does not assume clusters.

To quantify genetic distance between sample sites, we calculated pairwise F_{ST} values in R. Then, to assess different sources of landscape structure within species, including biogeographic barriers, we used *Poppr* 2.8.1 (Kamvar et al. 2014, 2015) to quantify the degree of genetic variance across the population hierarchy with a three-way analysis of molecular variance (AMOVA) following Weir and Cockerham (1984). Variance was assessed across pairwise F_{ST} values between individuals within sites, values averaged by sample site, and values averaged by lineages identified by sNMF. To assess the influence of catchment connectivity on gene flow within *T. laurina*, we performed a four-way AMOVA that included catchment membership within lineages. Significance was tested with a randomization test as per Excoffier et al. (1992), using 999 permutations.

Genetic diversity statistics were calculated and compared across sample sites within species and averaged across sites to compare overall diversity between species. The following estimates were calculated with the R package *diveR*sity (Keenan et al. 2013): observed heterozygosity (H_O), unbiased expected heterozygosity (uH_E), and allelic richness (A_R).

Palaeo-environment modelling

We used environmental niche modelling (ENM) to infer the geographic distribution of suitable palaeo-environments for each species, to test whether current and/or past habitat connectivity can explain observed patterns of genetic structure. There are a number of assumptions that reduce our confidence in niche projections, including the inability to account for the likelihood that some past environments had no modern analogues to train the models (Williams and Jackson 2007), or the possibility that the study species' current distributions are in disequilibrium with the environment due to dispersal constraints (Svenning and Skov 2007) or that they underwent changes in existing realized niche since the LGM (Worth et al. 2014). Nevertheless, a number of studies have found that such models corroborate genetic evidence for glacial refugia and post-glacial shifts (Mellick et al. 2012, 2014, 2013b; Ortego et al. 2015).

We modelled the current distribution of habitat suitability for each species using the maximum entropy algorithm implemented by MaxEnt 3.3.3 (Phillips et al. 2006; Phillips and Dudík 2008). Because widely distributed species are often composed of locally adapted populations with distinct environmental tolerances and potential ranges (Banta et al.

2012), intraspecific genotypes have been identified as useful units for climate envelope modelling (Eckert et al. 2009; Fournier-Level et al. 2011; Hancock et al. 2011). We produced separate models for the within-species lineages identified by sNMF (sensu Jezkova et al. 2009; Mellick et al. 2011; Hornsby and Matocq 2012; Banta et al. 2012), as well as models based on the full distribution of each species.

The full-species models were constructed using the same occurrence records, extent, and resolution as described for the niche models implemented in *Ecospat*. The lineage-based models were trained on a background area constrained to a 200 km radius around each occurrence point, to avoid very different climates inflating the strength of predictions. We qualitatively assessed the accuracy of predicted occurrences and used model-evaluation statistics to select sets of non-correlated bioclimatic and geomorphological variables for each lineage. Only sets of variables with a variance inflation factor ≤ 12 were used for each model (Powney et al. 2011) which was iteratively calculated using the R package *usdm* (Naimi 2013).

To produce palaeo-models for the LGM and HCO climate scenarios, we projected contemporary species-environment relationships onto General Circulation Models obtained from the Inter-comparison Project 5 data repository maintained by the Earth Survey Grid Federation, accessed via the Lawrence Livermore National Laboratory node (<https://esgf-node.llnl.gov/projects/esgf-llnl>; Supplementary Table S2). For each General Circulation Model, we ran 10 replicates under the cross-validation method with linear, product, and quadratic features. Current and palaeo-habitat suitability maps based on the logistic output of MaxEnt were generated to visualize habitat availability through time. We compared the output from each model, since the climate scenarios simulated by different General Circulation Models vary considerably (Whetton et al. 2015). We also calculated the mean logistic output scores across models to use as a consensus habitat suitability model in downstream analyses. Finally, we used the sum of the logistic output of each climatic period to estimate Holocene habitat suitability stability (*sensu* Devitt et al. 2013). Since the ENMs do not account for the reduced atmospheric CO₂ concentrations which would have exacerbated the physiological effects of aridity during the LGM, we take a conservative estimate of habitat suitability as ≥ 0.7 .

Landscape genetic analyses

We sought to test whether niche specialization differentiates the dispersal potential of the study species, and whether dispersal varies across the study area. First, we applied circuit theory to evaluate whether gene flow within lineages

reflects isolation-by-distance (IBD) or different isolation-by-resistance (IBR) scenarios. IBR assumes that habitat suitability constrains dispersal across spatially heterogeneous landscapes more than can be expected of geographic distance alone (McRae and Beier 2007). IBR is typically used to estimate animal movement across habitat networks, though it can be applied at a broader scale to evaluate dispersal as the number of migrants exchanged between subpopulations per generation (Shah and McRae 2008; Ortego et al. 2015).

We used CIRCUITSCAPE 4.0.5 to calculate resistance distance matrices between all pairs of population sample sites, considering an eight-neighbour cell connection scheme (Shah and McRae 2008). The resistance distance is calculated according to the minimum movement cost and weighted by the availability of alternative pathways. In summary, the resistance distance is small when two cells are connected by many paths with low resistance values and large when there are few paths with high resistance.

We used habitat suitability data (i.e. the mean logistic output of the ENMs) as conductance grids to calculate resistance values that reflect four IBR scenarios: (1) current habitat suitability ($IBR_{CURRENT}$); (2) HCO habitat suitability (IBR_{HCO}); (3) LGM habitat suitability (IBR_{LGM}); and (4) Holocene habitat suitability stability ($IBR_{STABILITY}$; see above). To model IBD, we calculated a matrix of log transformed Euclidean geographic distances between sampled populations. We modelled IBR and IBD separately for each lineage as well as across the full range of the study species. This enabled us to assess whether there is regional variation in landscape influences on the range dynamics of the species, and control for the confounding effect of biogeographic barriers on the pattern of IBD (Slatkin 1993; Rousset 1997; Garnier et al. 2004).

IBD and IBR matrices were tested against genetic distance matrices using multiple matrix regression with randomization (Wang 2013) implemented in the R package PopGenReport 3.0.0 (Adamack and Gruber 2014; Gruber and Adamack 2015) and partial Mantel tests in the package ncf 1.2–6 (Bjornstad and Cai 2018). We constructed and evaluated models with each possible combination of explanatory terms fitted. However, final models do not include >2 independent variables because multi-collinearity hampered interpretation of results. The coefficient of determination (r^2) indicates the overall model fit whilst the regression coefficient (β_n) indicates the strength of the association between linearized F_{ST} and each individual distance variable after other variables have been accounted for. Finally, for each lineage in each species, we performed a Pearson's correlation on population genetic diversity indices (A_R , H_O , and uH_E) with their latitude and $IBR_{STABILITY}$ SCORES.

Tests for range expansion

We sought to compare the study species in their potential for range expansion versus persistence in refugia. We used an approach developed by Peter and Slatkin (2013) that tests whether drift under population expansion can explain the observed genetic structure. This approach infers the strength of founder effects associated with spatial expansion and the most likely expansion origin, and tests significance against a null model of equilibrium IBD (Peter and Slatkin 2013, 2015).

The model assumes that present-day populations have expanded on a stepping-stone model from a single deme (i.e., refugium), assuming a founder effect (ke/Ne) for each colonization event and one generation of drift between events. In an island population model, Ne corresponds to the effective population size and ke corresponds to the effective number of founders on a given island. Given that we do not know the actual deme size of subpopulations for most species, the founder effect is arbitrarily re-scaled to 0.99. This enables us to compare expansions using the distance over which that founder effect occurs, where a low founder distance indicates a strong founder effect. Assuming $ke/Ne = 0.99$, the effective founder distance (d) is calculated as the deme size (in km) for which Ne is reduced by 1% in a founder event. As per the assumption of a single source population, we constructed separate models for the lineages identified by sNMF, which would have had distinct expansion origins (Peter and Slatkin 2013).

The model will detect weak or non-significant founder effects if range expansion was gradual, the species underwent long periods of post-expansion drift, or the species had multiple reticulate expansions per lineage. Based on results from an *Arabidopsis thaliana* dataset (Peter and Slatkin, 2015), we consider $d < 5$ km to indicate strong founder effects and $d > 25$ km to indicate weak founder effects.

Results

Environmental niche differentiation between species

Niche overlap is low between *Tristaniopsis collina* and *T. laurina* ($D = 0.311$), supporting the hypothesis that environmental preferences differ between the species. Niche equivalency was rejected ($P = 0.0198$) and niche similarity was greater than expected by chance ($P = 0.099$), indicating that the observed niche differentiation between species is a function of habitat selection rather than an artefact of underlying differences in available environments between the two species.

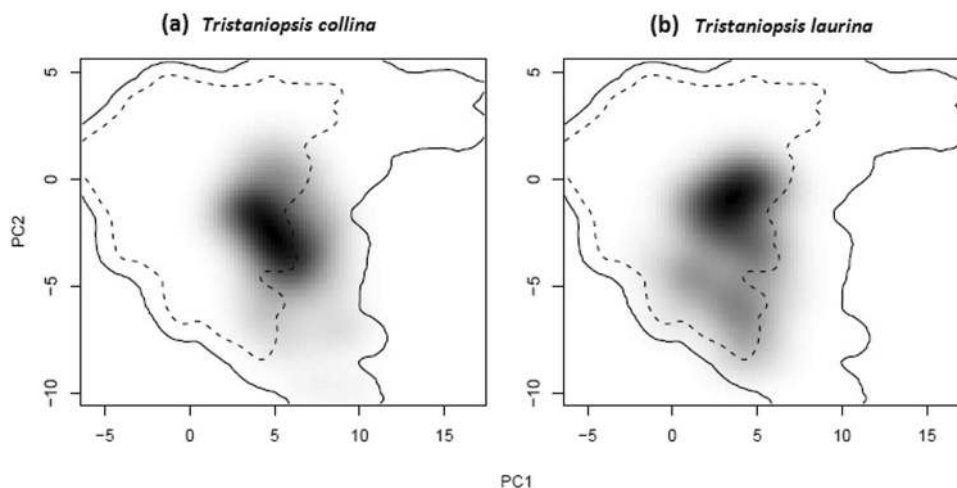


Fig. 2 A model of environmental niche occupancy (grey gradient) and availability across the distribution of **a** *Tristaniopsis collina*, and **b** *T. laurina*. The axes define environmental space in the model, according to the first two principal components that describe variance across twenty-three bioclimatic and seven geomorphological predictor variables. The solid line indicates 100% of available environments and the

dashed line shows the 50% most frequent available environments. The environmental niches of the two species differ according to tests of niche equivalency ($P = 0.020$) and niche similarity ($P = 0.099$). *Tristaniopsis laurina* shows greater niche breadth but a smaller core density of occurrences

The PCA separates the occurrence of *T. collina* and *T. laurina* in environmental space and the first two principal components explain 68.86% of the total environmental variation between the species (Fig. 2). The PC loadings of predictor variables indicate that *T. collina* occupies a cooler, wetter, and more aseasonal range of climates than does *T. laurina* (Supplementary Table S4). We found that *T. laurina* has a greater niche breadth (PC1 variance = 4.98, PC2 variance = 7.66) than does *T. collina* (PC1 variance = 3.311, PC2 variance = 4.64), indicative of broader bioclimatic tolerances.

Genotypic diversity and population structure

Genetic subdivision was detected between all populations of *T. collina* and *T. laurina*, based on pairwise population F_{ST} estimates ($P < 0.001$; Supplementary Tables S4–S5). Subdivision was slightly lower among populations of *T. collina* (mean $F_{ST} = 0.170$; Supplementary Table S5) than among those of *T. laurina* (mean $F_{ST} = 0.194$; Supplementary Table S6). This excludes populations north of the Hunter River Corridor, where *T. collina* has greater F_{ST} values than does *T. laurina*.

For *T. collina*, the cross-entropy evaluation implemented in sNMF suggests $K = 4$ –10 and the k -means analysis implemented in adegenet identified 3–5 clusters (Supplementary Figs. S1–S2). We assumed $K = 4$ in subsequent analyses of *T. collina* because this is the simplest most parsimonious model. The four ancestral lineages (*Shield Volcano*, *North*, *Central*, and *South*) are diverged across three biogeographic barriers:

Clarence River Corridor, Hunter River Corridor, and Cumberland Plain (Fig. 1b). However, a fifth cluster was identified in the Barrington region and also makes biogeographic sense. Both analyses identified three ancestral lineages in *T. laurina* (*North*, *Central*, and *South*; Supplementary Figs. S3–S4) bounded by two barriers (Hunter River Corridor and Cumberland Plain; Fig. 1c).

The mean population assignment proportions are generally high (0.724 in *T. collina* and 0.861 in *T. laurina*). If the clusters represent ancestral lineages as per the assumption of sNMF, both species show admixture indicative of secondary contact zones south of *Central* in the Illawarra plateau and to the north in the Barrington region (Fig. 1). This region either admixed in *T. collina* assuming $K = 4$ or differentiated due to drift under geographic isolation assuming $K = 5$.

The PCA ordinations identify the same major groupings as sNMF (albeit with hierarchical structure) and reveal opposite trends between the study species. Within *T. collina*, strong geographic structure is evident in *North*, which separates populations across the Manning River Valley and the Hunter River Corridor (PC1 = 16.98; Fig. 3a). Along PC2 (2.13), *Central* lacks structure and *South* shows moderate geographic structure. The primary source of variation in *T. laurina* is between populations separated by the Hunter River Corridor (PC1 = 15.28; Fig. 3b). Populations in the Hunter catchment also separate from other populations in *Central* along PC1. There is little geographic structure in *North*, and continuous variation within *South* along PC2 (2.74).

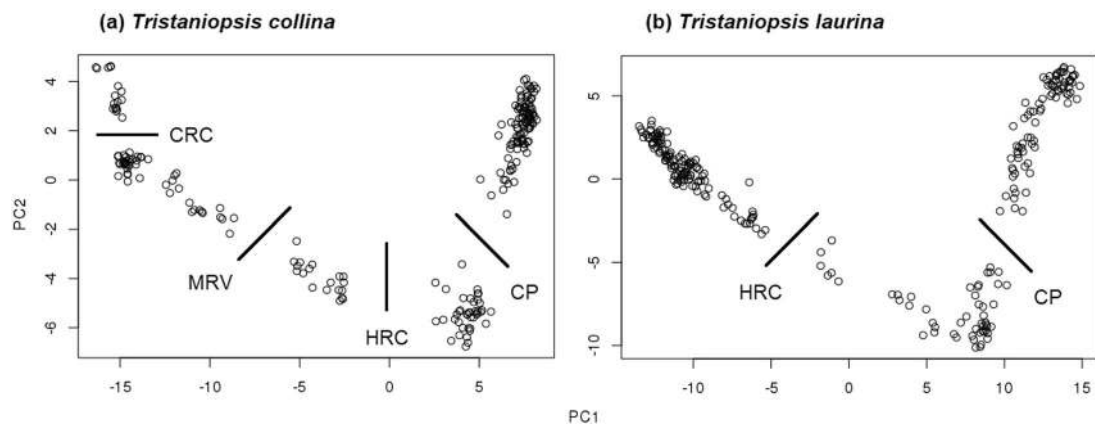


Fig. 3 Principal components analysis of genetic distance between **a** 204 samples of *Tristaniopsis collina* across 8,215 loci, and **b** 276 *T. laurina* samples across 10,883 loci. Lines indicate the Clarence River

Corridor (CRC), Manning River Valley (MRV), Hunter River Corridor (HRC), and Cumberland Plain (CP)

Table 1 Hierarchical analysis of molecular variance (AMOVA) for two species of *Tristaniopsis*

Species	Source of variance	% total variance	<i>P</i>
Three-way AMOVA			
<i>Tristaniopsis collina</i>	Among lineages	19.10	0.001
	Among populations	6.14	0.001
	Within populations	74.76	0.001
<i>Tristaniopsis laurina</i>	Among lineages	19.38	0.001
	Among populations	11.40	0.001
	Within populations	69.21	0.001
	Among catchments	17.07	0.001
	Among populations	9.05	0.001
Four-way AMOVA			
<i>Tristaniopsis collina</i>	Among lineages	18.96	0.001
	Among catchments	3.33	0.001
	Among populations	8.48	0.001
	Within populations	69.23	0.001

Lineages were identified by sNMF, assuming $K = 4$ in *T. collina* and $K = 3$ in *T. laurina*

The AMOVA revealed that the two study species have similar levels of structure across barriers, although greater within-lineage differentiation is apparent for *T. laurina* populations (Table 1). Among-catchment differentiation is an equivalent source of variation to lineage divergence in *T. laurina* when included as a separate variable in the three-way AMOVA. The four-way AMOVA indicates there is greater variation within catchments than between catchments, discounting the hypothesis that hydrochory facilitates long-distance dispersal within catchments. Finally, using Welch's *t*-test we found greater genetic diversity in *T. laurina* across all estimates and all lineages ($P < 0.001$; Supplementary Table S1), suggesting longer population persistence in this species.

Inference of post-LGM habitat shifts

The modelled present-day distributions of *Tristaniopsis* are consistent with their observed occurrences (excluding the full model of *T. laurina*), and the average area-under-the-curve scores (all models ≥ 0.929) indicate a good model fit (Supplementary Table S3). The full distribution models under-predicted habitat availability relative to the lineage trained models, though both methods generally agreed. Likewise, there was overall concordance between models derived from the different General Circulation Models. Excluding the LGM models for *T. laurina* North and South and the HCO models for *T. collina* South, visual inspection showed at least 75% of General Circulation Models predicted the same habitat suitability distributions for each lineage. However, some General Circulation Models were spatially inconsistent in the amount of habitat suitability predicted across the study region when compared to the lineage means.

Overall, the full-distribution and lineage-based ENMs indicate a larger and more stable environmental envelope for *T. laurina* than for *T. collina*, with contrasting habitat suitability shifts since the LGM (Fig. 4; Supplementary Fig. S5). The models show long-term habitat barriers across the Clarence River Corridor, Hunter River Corridor, and Cumberland Plain, which is consistent with the lineage boundaries identified in *T. collina* assuming $K = 4$. Interestingly, *T. laurina* shows greater connectivity across these barriers, despite the greater genetic differentiation within this species.

For *T. collina*, we produced a combined *Shield Volcano* and *North* model because there were insufficient data points to train a separate model for *Shield Volcano*. The models indicate putative refugia (habitat suitability > 0.7) at three upland regions for *Shield Volcano-North* (Fig. 4a).

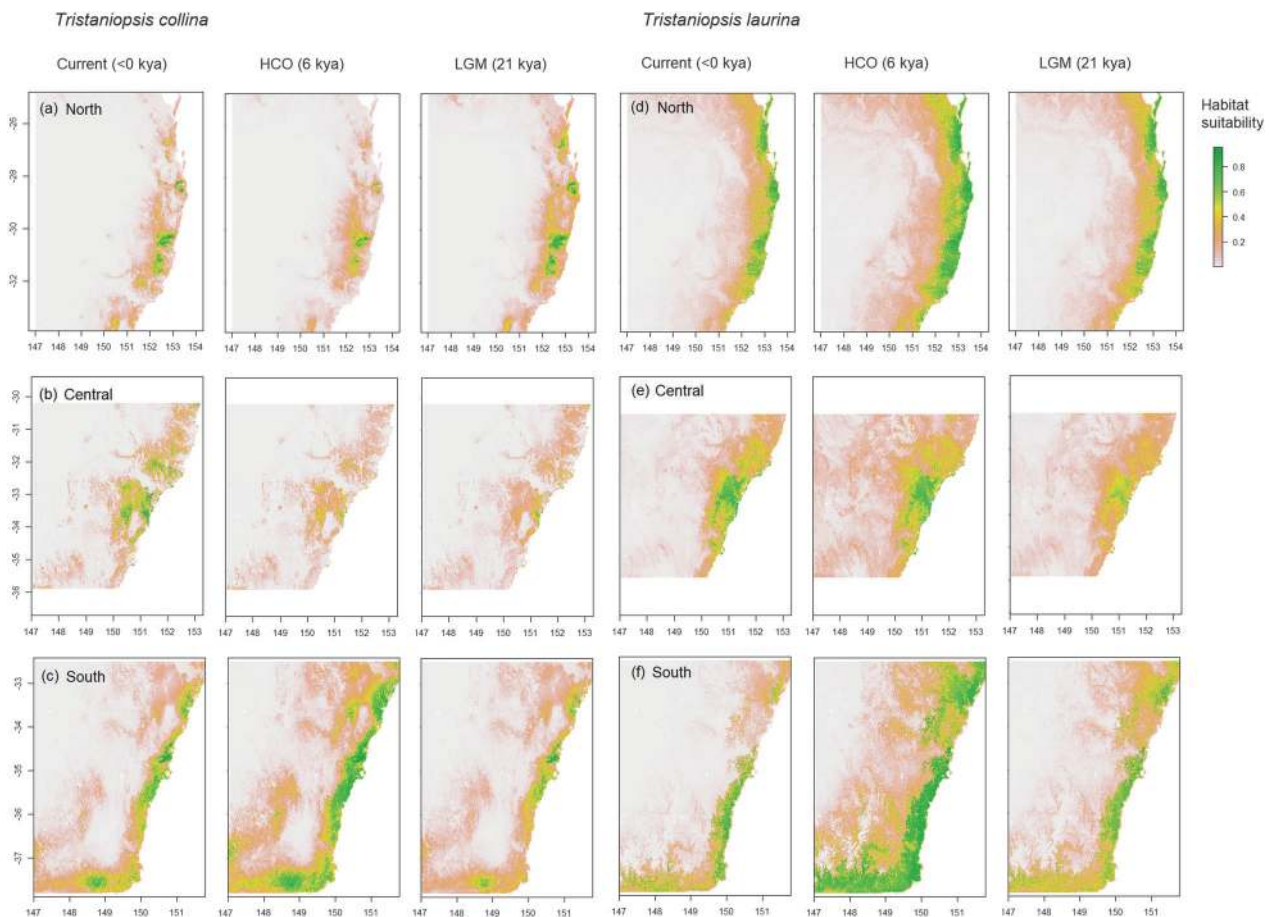


Fig. 4 Environmental niche modelling for three lineages of *Tristaniopsis collina* (a–c) and *T. laurina* (d–f) in eastern New South Wales. For each lineage, three Holocene climate scenarios are shown: the Last Glacial Maximum (LGM; c. 21,000 years ago), the Holocene Climatic Optimum (HCO; c. 6000 years ago), and the present day. The

predictor variables and climatic models used for the LGM and HCO distributions are listed in Supplementary Tables S2 and S3. The colour scale refers to the logistic probability (range: 0–1) of habitat suitability in the study area

However, significant local and regional habitat contractions were projected for the HCO (Fig. 4a). The ENMs for *Central* projected low LGM and HCO habitat suitability (Fig. 4b), though identified microrefugia on either side of the Hunter River Corridor. The models indicate that the lineage underwent a large-scale habitat expansion between the HCO and the present day. The models for *South* suggest fairly stable fragments of suitable habitat across each period, though a rapid expansion of habitat availability was inferred between the LGM and HCO (Fig. 4c). All ENMs (including trial models with different predictor variables) identified suitable habitat in Victoria. This is outside the current range of *T. collina* and may indicate range disequilibrium with the environment.

From the *North* model for *T. laurina*, we identified three large areas of suitable habitat that expanded between the LGM and HCO; and contracted again in the present day (Fig. 4d). We did not find suitable LGM habitat in *Central* (Fig. 4e), and the models suggest that the species underwent significant expansion from coastal microrefugia to inland

regions, particularly during the HCO. Finally, the models for *South* identify fragments of refugia in southeast Victoria and along the extent of the southern NSW coastline (Fig. 4f). The models also suggest significant habitat expansion from refugia between the LGM and HCO, and a subsequent contraction under the current climate.

Landscape genetic analyses

Due to multicollinearity between the distance matrices, we were not able to reliably assess models with more than two independent variables. We found an overall weak influence of IBD and IBR variables on F_{ST} in both species. Support from the single GCM models was mixed. While the regression coefficient of IBR variables was often congruent with the mean model, many lost significance with the inclusion of IBD. While this reduced our ability to assess the relative contribution of each variable to genetic isolation, we were able to infer that dispersal constraints slightly differ among species, and among lineages within species (Table 2).

Table 2 Partial Mantel correlation and multiple matrix regression (MMRR) coefficients between genetic distance (F_{ST}) and mean habitat resistance (IBR) and geographic distance (IBD) matrices

Model	Partial Mantel		MMRR			%GCMs
	R^2 (IBR)	R^2 (IBD)	β_n (IBR)	β_n (IBD)	R^2 (model)	
<i>Tristaniopsis collina</i>						
Full range						
F_{ST} —IBR _{CURRENT} /IBD	0.649**	0.082 ns	0.032***	0.046 ns	0.789***	—
F_{ST} —IBR _{HCO} /IBD	0.701**	0.160**	0.014***	0.076 **	0.815***	75
F_{ST} —IBR _{LGM} /IBD	0.493**	0.225**	0.02***	0.147**	0.725***	50
F_{ST} —IBR _{STABILITY} /IBD	0.678**	0.017 ns	0.085***	0.009 ns	0.803***	—
Shield Volcano—North						
F_{ST} —IBR _{CURRENT} /IBD	0.521**	0.200 ns	0.015**	0.043 ns	0.653***	—
F_{ST} —IBR _{HCO} /IBD	0.570**	0.174 ns	0.015**	0.035 ns	0.678***	100
F_{ST} —IBR _{LGM} /IBD	0.606**	0.002 ns	0.043**	>0.000 ns	0.699***	100
F_{ST} —IBR _{STABILITY} /IBD	0.599**	0.041 ns	0.083**	0.009 ns	0.695***	—
South						
F_{ST} —IBR _{LGM} /IBD	0.391*	−0.067ns	0.012*	−0.009ns	0.318*	50
<i>Tristaniopsis laurina</i>						
Full range						
F_{ST} —IBR _{CURRENT} /IBD	0.610**	0.127**	0.073***	0.061**	0.768***	—
F_{ST} —IBR _{HCO} /IBD	0.617**	0.030 ns	0.072***	0.016 ns	0.771***	100
F_{ST} —IBR _{LGM} /IBD	0.596**	0.165**	0.030***	0.078***	0.762***	40
F_{ST} —IBR _{STABILITY} /IBD	0.631**	0.053 ns	0.152***	0.026 ns	0.778***	—
North						
F_{ST} —IBR _{CURRENT} /IBD	0.069 ns	0.243**	0.005 ns	0.052*	0.320***	—

IBR is estimated habitat resistance for the Last Glacial Maximum (LGM), the Holocene Climatic Optimum (HCO), current day (CURRENT), and summed across periods (STABILITY)

The regression coefficient (β_n) indicates the strength of the association between F_{ST} and the distance variable, and the coefficient of determination (R^2) indicates overall model fit

Habitat resistances were calculated from the mean habitat suitability inferred from 10 Generalized Circulation Models (GCMs). %GCMs indicates the proportion of individual GCMs that yielded the same result as the mean

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant

The effect of IBD on genetic differentiation within *T. collina* is small and its significance was usually lost when IBR variables were included in the models. IBR_{HCO} and IBR_{STABILITY} best explained pairwise F_{ST} across the full range of *T. collina* as did IBR_{LGM} in *Shield Volcano—North*; though all IBR variables were significant. For the other lineages, IBR_{LGM} in *South* was the only significant variable when other variables were controlled for. The IBR variables had a greater influence on the full range model of *T. laurina* compared with *T. collina*, and IBR_{STABILITY} was the most influential. There was no support for the influence of IBR variables in the individual lineages. We found a moderate influence of IBD within *Sydney* and *South* in the partial mantels, though not in the multiple matrix regression models when IBR variables were included.

For both species, we found a significant negative correlation between A_R and uH_E with latitude in *North* and a significant positive correlation in *South* (Table 3). The same

Table 3 Pearson's correlation coefficients calculated for latitude and population genetic diversity estimates allelic richness (A_R), observed heterozygosity (H_O) and un-biased expected heterozygosity (uH_E) for *Tristaniopsis* lineages

Species	Lineage	A_R	H_O	uH_E
<i>T. collina</i>	Full	−0.073ns	−0.334ns	−0.502**
	North	−0.929***	−0.134ns	−0.881***
	Syd	−0.821*	0.236ns	−0.129ns
	South	0.701**	−0.269ns	0.666**
<i>T. laurina</i>	Full	0.169ns	0.375**	0.155ns
	North	−0.804***	−0.622**	−0.798***
	Syd	0.428ns	0.504ns	0.426ns
	South	0.538*	0.551*	0.551*

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant

trends were also significant for H_O in *T. laurina*. This suggests that genetic diversity increases at lineage boundaries with *Central*, potentially due to admixture between

Table 4 Range expansion and founder effect test results for *Tristaniopsis*

Species	Lineage	Latitude	Longitude	Altitude (m)	<i>q</i>	<i>d</i> (km)	<i>R</i> ²	<i>P</i>
<i>Tristaniopsis collina</i>	Shield Volcano-North (+Barrington)	-28.5697	151.6017	670	0.0009	5.4624	0.936	<0.000
	Shield Volcano-North (-Barrington)	-28.7895	152.3171	540	0.0008	6.6840	0.886	<0.000
	Central (+Barrington)	-32.3666	150.3608	220	0.0010	5.1637	0.459	0.446
	Central (-Barrington)	-33.2605	150.8189	290	0.0023	2.2337	0.967	<0.000
	South	-36.5117	149.9736	140	0.0001	32.5417	0.411	<0.000
<i>Tristaniopsis laurina</i>	North	-28.9402	153.5230	5	0.0002	20.6609	0.712	<0.000
	Central	-33.9326	151.0987	20	0.0002	28.2944	0.222	0.648
	South	-36.5698	149.8996	215	0.0005	10.9072	0.428	<0.000

Latitude, longitude and altitude indicate location of predicted origin of range expansion for each lineage. *q* is the directionality index, which positively increases with distance from origin of range expansion and approaches zero with time since expansion and/or migration between demes. *d* is the effective founder distance in km (the deme size for which *N_e* is reduced by 1% during a founder event) and a low value indicates a strong founder effect. *R_{sq}* of the regression of *q* versus difference in distance from origin. Bonferroni corrected *P*

P < 0.001

lineages. We did not find significant correlations between diversity values and *IBR_{STABILITY}* (all *P* > 0.1).

Range expansion models

For *T. collina*, we produced a single *Shield Volcano-North* model because there were insufficient data points to produce separate models for each of the northern groupings identified in the PCA. We also included models of the *Central* and *Shield Volcano-North* groups both with and without the Barrington region, owing to the uncertain boundary between the two lineages in this species. Overall, there was strong support (*P* < 0.0001) for the serial-founder expansion model among *T. collina* lineages, indicating rapid or recent range expansion (Table 4). Models for *Shield Volcano-North* inferred a primarily southward expansion originating west of the Border Ranges; though this is not consistent with the multiple refugia identified from by the palaeo-environment models. The strongest founder effect was detected in *Central* (without Barrington), and we inferred the expansion origin from a mid-altitude site in the Sydney Basin to montane areas in the Greater Blue Mountains. This is consistent with the habitat expansion inferred from the palaeo-environment models. For *South*, we inferred a range expansion from the southernmost range limit of *T. collina*. However, the low *R*² (0.4113) reduces our confidence in the predicted site of origin. The weak founder effects in this lineage are consistent with the greater habitat connectivity and stability inferred from the ENMs.

By comparison, founder effects in *T. laurina* *North* and *South* are one order of magnitude weaker (Table 4); suggesting older, slower, or more reticulate range expansion scenarios in this species. For *North*, we inferred a predominantly north-to-south range expansion from a lowland coastal site. The weak founder effects are consistent with the stable habitat connectivity inferred from the ENMs. For

South, we inferred a multidirectional expansion from the far south coast of NSW. The moderate founder effects are not consistent with the high habitat availability inferred for this region. Model support was not significant for *Central* (*P* < 0.01) which indicates that the observed structure in this lineage cannot be differentiated from equilibrium isolation by distance.

Discussion

A broader aim of this study was to investigate the relative importance of dispersal versus persistence on the range dynamics of long-lived trees, and whether this relates to habitat preference. We found that the tree species *Tristaniopsis collina* and *T. laurina* have similar restrictions across major biogeographic barriers and overall genetic structure, despite evidence of significant environmental niche differentiation and contrasting habitat shifts under Holocene climate change. However, our range expansion models and landscape genetic analyses do reveal cryptic differences in the dispersal potential of the study species and their persistence in refugia. We discuss these findings in reference to the bioclimatic preferences, habitat connectivity and recruitment of our two study species.

Niche divergence in *Tristaniopsis*

As a first step towards demonstrating the impact of niche preference on range dynamics, we verified that environmental niche separation between the study species is a function of habitat selection. The species are significantly differentiated across environmental space, and we confirmed a smaller bioclimatic niche for *T. collina*. This can be attributed to the tendency of *T. collina* to occupy higher altitudes across its range, where it encounters lower

temperatures and greater precipitation than does *T. laurina*. However, the coarse resolution of the bioclimatic variables must be interpreted with caution. Considering that *T. laurina* is known to be drought sensitive (Mellick 1990a), its greater distribution in slightly warmer-drier climates than *T. collina* should not be taken to indicate that the species is better adapted to those conditions. A more likely explanation is that the riparian habitats of *T. laurina* are sometimes nested within areas that receive less precipitation than would otherwise be suitable. So, although *T. laurina* is spatially restricted at a local scale, the riparian microclimate enables the species to occupy a broader geographic range.

Equivalent dispersal across ancient habitat barriers

We used multiple clustering methods to investigate the influence of ancient habitat barriers on within-species divergence. Congruence with the PCA ordination suggests that the ancestral lineages presented in Fig. 1 are a good approximation of the overarching genetic structure of the study species, though hierarchical structure north of the Hunter may have led to an under-estimation of K in *T. collina*. The continuous genetic variation observed within *T. laurina* lineages suggests $K=3$ is most parsimonious. However, the algorithm implemented by sNMF cannot differentiate between recent admixture and other demographic histories. Consequently, admixed populations might be the outcome of admixture with an extinct lineage or a recent bottleneck (Lawson et al. 2018) rather than secondary contact. Given our thorough sample scheme, it is unlikely the results have been confounded by un-sampled genotypes.

We anticipated that environmental niche differentiation and contrasting range shifts would have varied the influence of biogeographic barriers on the study species. While our palaeo-environment models suggest that the two species had differing degrees of habitat availability over the last 21,000 years, both species show divergence across dry barriers north and south of Sydney that likely pre-dates the LGM. This includes the Cumberland Plain, a low altitude 2750 km² basin located in the rain shadow between the Greater Blue Mountains and coastal Sydney (Fig. 1). To our knowledge, this study is the first to highlight the region as an ancient-dry genetic barrier, and it is interesting that such restrictions are not evident in rainforest trees genotyped from the region (e.g. Mellick et al. 2011; Heslewood et al. 2014).

Our expectation that dispersal mechanism or environmental niche would differentiate the impact of biogeographic barriers on the study species was not supported. Although we found that catchment connectivity facilitates gene flow within *T. laurina*, the overall equivalent partitioning of genetic diversity within each of the study species

suggests that they are characterized by similar dispersal potential (Duminil et al., 2007). This either discounts hydrochory as a frequent mechanism of long-distance dispersal in *T. laurina* or suggests other factors regulate gene flow (see section below). Other studies have demonstrated that dispersal traits such as fruit size (Rossetto et al. 2009; Rossetto et al. 2015a) and fruit fleshiness (Rossetto, Mcpherson, et al. 2015; Worth et al. 2017) have a greater influence on migration across barriers. Likewise, compared with co-distributed trees from wet versus dry forests (Milner et al. 2012; Worth et al. 2017) or nutrient-rich versus nutrient-poor soils (Rossetto et al. 2009), niche differentiation did not significantly vary barrier effects between the study species. Nevertheless, higher rainfall requirements can account for the greater structure of *T. collina* across the dry valley systems of northern NSW. In contrast, the palaeo-models suggest that these barriers were less important for *T. laurina* after the LGM.

Dispersal or persistence under Holocene climate change

The palaeo-environment models and genetic data indicate that range shifts through the Holocene can partially account for genetic variation within *T. collina* and we deduce that greater climate sensitivity has reduced its persistence potential compared with *T. laurina*. An increasing number of studies have identified high-altitude LGM refugia for tree species in areas outside their current bioclimatic limits (Nevill et al. 2014; Zeng et al. 2015). Yet for *T. collina*, we inferred a serial-founder range expansion from midland refugia to high-altitude localities in *Central*. This is consistent with palynological surveys in the region that have identified the LGM treeline to be as low as 1000 m (Hesse et al. 2003) (Sweller and Martin 2001). As a gravity-dispersed tree, range expansion in *T. collina* is likely to have occurred through a series of stepping-stone colonization events. This demonstrates that tree species are capable of rapid climate-driven range shifts even in the absence of long-distance dispersal mechanisms.

In contrast, *T. laurina* exhibits slightly higher genetic diversity and stronger population structure more consistent with spatial conservatism and periodic isolation (Hewitt 1996) than with rapid range expansion. Combined with the palaeo-environment models, this suggests that persistence in multiple refugia has maintained a relatively stable distribution of *T. laurina* through the Holocene. Meanwhile, weak founder effects suggest that as conditions improved during the HCO, the species underwent only gradual and/or localized expansions. Localized elevational shifts have been inferred for montane trees across a range of environments in response to past climatic change (Gugger et al. 2013; Mellick et al. 2013b, 2014; Nevill et al. 2014). Here we find

evidence for in situ persistence during the last interglacial, which supports the hypothesis that riparian sites can provide important microrefugia (de Lafontaine et al. 2014) particularly for lowland species (Aide and Rivera 1998).

Following observations of co-distributed trees in other ecosystems, we anticipated that genetic structure within *Tristaniopsis* would reflect their differing sensitivities to Pleistocene climatic change (Collevatti et al. 2001, 2013, 2014; Ramos et al. 2007; Novaes et al. 2010, 2013; Souza et al. 2017). The greater structure in *T. laurina* was therefore surprising given its broader environmental niche and potential for connectivity along riparian corridors. This disparity implies that species differences are not fully explained by their past or current habitat availability. We hypothesize that specialized recruitment traits limit the colonization success of *T. laurina* and reduce genetic connectivity relative to *T. collina*. For instance, *T. laurina* seedlings are adapted to the nutrient and light pulses that follow flood-disturbance events (Melick 1990a, b) and so colonization is rare in the absence of high rainfall and disturbance (Melick and Ashton 1991). To explore this hypothesis, it is worth investigating whether *T. collina* seedlings germinate and colonize new habitats more readily than *T. laurina*.

Like other species that have had a relatively continuous (albeit fragmented) distribution of suitable habitat since the LGM (e.g. Ortego et al. 2015), we did not find a relationship between genetic diversity and habitat stability. This contrasts with tree species that underwent more dramatic range shifts from a large central refugium, in which diversity is either associated with habitat stability or distance from a refugium core (Collevatti et al. 2013; Tsuda et al. 2015; Zeng et al. 2015; Souza et al. 2017; Kim et al. 2018). However, in both *Tristaniopsis* species, we did find a latitudinal cline in diversity that increased at sites of admixture between the putative lineages, supporting a scenario of secondary contact following Holocene warming. Similar patterns of elevated diversity in admixed zones has been widely reported in trees from the Northern Hemisphere (Comps et al. 2001; Walter and Epperson 2001; Petit et al. 2003; Heuertz et al. 2004; Sakaguchi et al. 2011; Lee et al. 2014; Havrdová et al. 2015).

As we found a weak signal IBD and mixed support for IBR in both our study species, we must consider potential shortcomings in their palaeo-environment models. This could include overfitting or inappropriate variable selection, as we only calculated resistance matrices from one set of variables per lineage. It is also possible that the genetic structure in the species is more closely associated with the climate of other periods than those explored in the present study. Finally, we acknowledge that other population models might be more appropriate for our species. For instance, isolation-by-environment is widely reported in

plant species (Sexton et al. 2014; Wang and Bradburd 2014). Alternatively, selection against migrants can reinforce founder effects created by range expansions, and drive a pattern of isolation-by-colonization that overrides the influence of environmental gradients (Orsini et al. 2013).

Range dynamics vary between regions

Finally, we have demonstrated that climate-driven range shifts can vary significantly across the distribution of widespread species. This was particularly evident among the different lineages of *T. collina*. Regional differences can be explained in terms of the latitudinal climatic gradient along eastern Australia that would have been differently affected by Holocene warming, as well as the spatial variation in topographic relief.

Tristaniopsis laurina also showed regional differentiation. As has been demonstrated in other riparian plants, mountain ridges between rivers act as genetic barriers whilst river valleys act as corridors for gene flow (Tero et al. 2003; Fer and Hroudava 2008; Wei et al. 2013; Werth and Scheidegger 2014). Following this, the greater genetic structure within *South* might be attributed to the more dissected landscape in which the lineage is located, compared with *North* where low topographic relief across extensive coastal plains is likely to facilitate greater dispersal within and between catchments.

Conclusions

This study investigated environmental niche partitioning and its impact on the range dynamics of two widely distributed, closely related sympatric trees in response to Holocene climate change. We conclude that riparian specialization has enabled *Tristaniopsis laurina* to occupy a broader climatic envelope and persist in multiple refugia across its range, while specialized recruitment traits potentially limit colonization of new habitat. In contrast, a narrow climatic niche has driven a history of habitat instability and larger-scale range shifts for *T. collina* throughout the Holocene. However as both species had refugia across their respective ranges, we can expect more dramatic differences in the range dynamics of species that occupy different soil types or biomes.

The patterns observed in *Tristaniopsis* have several implications for the study of range shifts and evolution in response to climate change. First, we have demonstrated cryptic differences in the historical ranges of species with present-day sympatry and similar biogeographic restrictions. This reveals how divergent processes can produce similar distributional patterns and highlights the utility of SNP-based demographic models to differentiate between

alternative drivers of population structure, such as drift via founder effects versus long-term geographic isolation. We also found that a greater niche breadth and capacity for long-distance dispersal does not necessarily enhance species' migration across habitat barriers or promote post-glacial range expansion. Finally, our results demonstrate that spatial variation in landscape barriers and climatic gradients can create regional differences in the range dynamics of widely distributed species.

Further research is needed to address some of the uncertainties in our study. In particular, the history of lineage divergence and admixture requires clarification. The mixed support for IBR and weak influence of IBD also suggests that other potential drivers of genetic variation need to be explored. Adaptive divergence could be frequent within species like *T. laurina* that have experienced local climate-driven range shifts but maintained stable ranges over time (Gugger et al. 2013; Ortego et al. 2015). Coalescent analyses can help verify the within-species lineages we identified and test whether the weak founder effects in *T. laurina* reflect a history of gradual, localized and/or ancient expansions. This could be combined with gene-environment association analyses to investigate climate adaptation as an alternative driver of population structure, and whether this differs between the two species. Finally, germination trials are required to test whether recruitment traits differentiate the colonization and range dynamics of *T. collina* and *T. laurina*.

Data archiving statement

Genomic data in the form of binary-coded SNPs (DArTseq) and geographic coordinates for all samples are available from Dryad: <https://doi.org/10.5061/dryad.0p6bj53>

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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