

Article

Post-Glacial Spatial Dynamics in a Rainforest Biodiversity Hot Spot

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Received: 21 November 2012; in revised form: 26 February 2013 / Accepted: 14 March 2013/

Published: 20 March 2013

Abstract: Here we investigate the interaction between ecology and climate concerning the distribution of rainforest species differentially distributed along altitudinal gradients of eastern Australia. The potential distributions of the two species closely associated with different rainforest types were modelled to infer the potential contribution of post-glacial warming on spatial distribution and altitudinal range shift. *Nothofagus moorei* is an integral element of cool temperate rainforest, including cloud forests at high elevation. This distinct climatic envelope is at increased risk with future global warming. *Elaeocarpus grandis* on the other hand is a lowland species and typical element of subtropical rainforest occupying a climatic envelope that may shift upwards into areas currently occupied by *N. moorei*. Climate envelope models were used to infer range shift differences between the two species in the past (21 thousand years ago), current and future (2050) scenarios, and to provide a framework to explain observed genetic diversity/structure of both species. The models suggest continuing contraction of the highland cool temperate climatic envelope and expansion of the lowland warm subtropical envelope, with both showing a core average increase in elevation in response to post-glacial warming. Spatial and altitudinal overlap between the species climatic envelopes was at a maximum during the last glacial maximum and is predicted to be a minimum at 2050.

Keywords: Altitudinal range shift; cool temperate rainforest; *Elaeocarpus grandis*; MtWarning Caldera; *Nothofagus moorei*; post-glacial warming; warm subtropical rainforest

1. Introduction

The far-eastern rainforests of Australia occur at the junction between the temperate and tropical climatic regions (32–25°S), and the area is a World Heritage listed biodiversity hotspot (*i.e.*, Central Eastern Rainforest Reserves of Australia). This high biodiversity is due to tropical, subtropical (lowland) and temperate rainforest (highland) alliances occurring in close-proximity [1]. It is generally assumed that distributional differences in rainforest communities are primarily a result of altitude and other abiotic gradients [2,3]. Within this zone of climatic overlap, subtropical genera are found in the moister habitats of the wet gullies of the eastern slopes of the ranges and on the coastal lowlands, while temperate genera form more open habitats on higher slopes where temperatures fall below those suitable for tropical species [4].

These rainforests show altitudinal changes in floristic community structure along the latitudinal gradient of the Great Dividing Range (GDR) of eastern Australia (e.g., some highland rainforest elements in the warmer north, occupy lowland areas in the cooler south [5]). Community expansions/contractions along altitudinal gradients in response to the climatic fluctuations of the Quaternary have allowed for periods of isolation (genetic drift) and migration (admixture) among latitudinal dispersed rainforest species [6]. In this system, a rainforest species' dispersal ability [7–9] is important in explaining the difference between its potential and observed distribution.

Plot-based studies monitoring climate-driven floristic shift in Australian subtropical rainforests have been largely inconclusive [10], and indicate that tree line evidence of global warming from the northern hemisphere [11,12] is unlikely to be found in the east Australian rainforest systems. Rather, evidence of temporal community turnover in response to climate from fossil observations [13] helps to explain current spatial division among rainforest types along altitudinal gradients (e.g., past lowland climates persist in mountainous regions). The spatial conservatism and persistence of some rainforest lineages points to localised environmental stability and highlights the importance of adaptive potential and selective tolerance to climate change [14,15]. A number of recent case studies show that the tension between persistence and dispersal (often in combination with abiotic factors) is an important mechanism contributing to the survival and distribution of rainforest species [7,8].

1.1. *Nothofagus moorei* and Highland Temperate Rainforests

Nothofagus moorei (F.Muell.) Krasser is a member of a quintessential Gondwanan genus represented in the fossil record [16–18]. The palaeoecological history of *Nothofagus* is well documented [16,17,19–22]. The species is frost resistant to –8 °C [21,22] and is now restricted to cool temperate rainforest at high elevation (c. 500–1550 m above sea-level) along the GDR north of the Hunter River Valley (NSW) and south from the McPherson Ranges (south Queensland). These temperate rainforests are typically situated on well-watered slopes with an eastern to southern aspect and, in the southern range of species, extend to small basins or other areas sheltered from desiccating

winds [23]. Orographic uplift along the range provides precipitation throughout the year that has maintained these ancestral communities, *i.e.*, annual precipitation, 1633 ± 325 mm, with relatively minor variation between mean winter and summer rainfall, *i.e.*, precipitation seasonality, 34 ± 11 mm [21]. Fog deposition provides the equivalent of an additional 40% of rainfall to these rainforests as measured using a conventional rain gauge [24]. *Nothofagus moorei* has sufficient temperature tolerance to persist in cooler and more seasonal climates, though is likely to have reduced growth rates and competitive ability in climates with drier summers [21].

The eastern temperate rainforests of Australia feature habitat islands that are usually fringed by subtropical and drier rainforests at lower elevation. Cool temperate rainforests along the GDR include cloud forests and their associated rich epiphytic endemism. More than 50 species of climbers and over 40 epiphytes and lithophytes are known to be associated with *N. moorei* forests, including a number of endemic species [25], suggesting the presence of a distinctive temperate floristic assemblage which characterises the principal domains of *N. moorei* [26].

The biogeography of *Nothofagus* suggests the genus rafted north (50–15 million years ago, Ma) on fragments of east Gondwana [19,20,27,28]. The best fossil records of *Nothofagus* offer information on past distribution and ecological associations that strongly suggest past climates have had an impact on the current distribution, and that species-specific traits including coppicing has allowed *Nothofagus* to persist in habitat of low suitability for long periods of time [29].

Reported genetic structure in *N. moorei* [30,31] is likely a signature of reduced gene flow among highland areas, potentially a consequence of climatic and biotic shifts between the last glacial maximum (LGM: 21 thousand years ago, ka) and the current period. Narrow range, poor dispersal ability and restriction to cool temperate rainforest, suggests the continued persistence of *N. moorei* populations could be at risk from global climate change. For instance, the lack of sufficient altitudinal relief along its northern range could threaten localised persistence, and lead to a significant loss of genetic variation [31]. Although sufficient temperature tolerance in *N. moorei* provides some resistance to climate warming, the species is especially vulnerable due to its highly fragmented distribution and low genetic connectivity between population groups. The co-occurrence of both high diversity and clonality in the northern McPherson Ranges populations (e.g., Mt Warning Caldera, The Lamington and Border Ranges National Parks) suggests increased disturbance and reduced recruitment in comparison to southern population groups [29,30]. The extremely long life-cycle due to coppicing (*i.e.*, clonality), suggest that old *N. moorei* trees could act as long-term genetic reservoirs thus explaining the high levels of remaining diversity [30].

1.2. *Elaeocarpus grandis* and Lowland Subtropical Rainforests

Elaeocarpus grandis (F.Muell.) is a long-lived early successional rainforest tree. It is synonymised with *E. angustifolius* that has an inter-continental range from India to New Caledonia [32], possibly a result of its good dispersal ability, fast-growth and long-life cycle. The species' physiology is well adapted to warm-wet conditions with close association to subtropical rainforests, which have been extensively cleared in lowland areas of eastern Australia [33,34]. *Elaeocarpus grandis* is specifically associated with complex notophyll vine forest [35], one of many types of subtropical rainforest occurring in eastern Australia. Woody vines or lianas are an element of sub-tropical rainforests and

other sub-class floristic alliances [1,34,36] which, together with tropical rainforests, are distributed throughout the warm-wet regions of the world, where low seasonality, ample sunlight and high precipitation support the occurrence of these voracious ecosystems.

A detailed phylogenetic study of the predominantly southern family Elaeocarpaceae provides strong evidence against a simple vicariant radiation of extant diversity [37]. Long-distance dispersal since the mid-Oligocene (28 Ma) to New Zealand [37] supports the notion of dispersal having a significant influence on extant distributions in the Southern Hemisphere [38,39]. The Elaeocarpaceae is a Gondwanan lineage with an extensive fossil history within Australia [40,41]. *Elaeocarpus* has broadly colonised lowland equatorial regions, and current distributional patterns in some species suggest possible re-colonisation of the Australian continent from the north.

1.3. Aims

The study aims to understand the impact of climate on two long-lived trees representing contrasting rainforest communities differentially distributed along altitudinal gradients of eastern Australia. Furthermore, the study aims to associate genetic patterns to the ecological and functional strategies of each species. The specific aims of the study are:

To investigate if current and historical climate envelope models can provide an explanation for the observed differences in the species' distribution and genetic diversity/structure particularly in light of contrasting successional and dispersal strategies.

To predict the spatial extent of habitat suitability for the end of this century based on the current distribution of *Nothofagus moorei* and *Elaeocarpus grandis*.

2. Results and Discussion

2.1. Post-Glacial Changes in Modelled Climate Suitability

MAXENT models for both species were found to be of high quality as measured by the area under the curve (AUC) statistic. For *N. moorei* the average AUC for the replicate runs was 0.989 (SD \pm 0.007). For *E. grandis* the AUC for the replicate runs was 0.982 (SD \pm 0.010).

Analysis of variable contribution indicated that for the cool temperate *Nothofagus moorei*: precipitation of the warmest quarter explained 24% (this accounted for 44% of the permutation importance), precipitation of the driest quarter explained 21%, mean temperature of the warmest quarter explained 7% and maximum temperature of the driest month explained 7% of the current distribution. Analysis of variable contribution indicated that for *E. grandis* (subtropical rainforest): annual precipitation explained 35% (this accounted for 91% of the permutation importance), mean temperature of the coldest quarter explained 27%, precipitation of the wettest quarter 10% and precipitation of the warmest quarter 8% of the current distribution.

The models predict that the climatic envelope of *N. moorei* has consistently contracted since the Last Glacial Maximum (LGM, 21 ka), while the climatic envelope supporting *E. grandis* has consistently expanded since the LGM (Figure 1).

Figure 1. Climate envelope models (potential range) for *Nothofagus moorei* (blue) and *Elaeocarpus grandis* (yellow) in eastern Australia, including the Mt Warning Caldera (g, h, and i), based on the Model for Interdisciplinary Research on Climate (MIROC 3.2.2) global climatic model for 21 thousand years ago (a, d and g) Last Glacial Maximum time period, the current time period (b, e and h) based on WorldClim data (1966–present) and an average of 13 global climatic models for 2050 (c, f and i: A2 greenhouse gas scenario). The core (high) habitat suitability predictions (g, h, and i; 60%–100%), show (i: 2050) The Lamington and Border Ranges National Parks (northwestern and western slopes of the Mt Warning Caldera respectively) will have small areas of high habitat suitability for *N. moorei* (blue). Areas of higher elevation are indicated by darker shading and areas of lower elevation are indicated by lighter shading. The species current occurrences (realised range) are shown in Figure 3a and b.

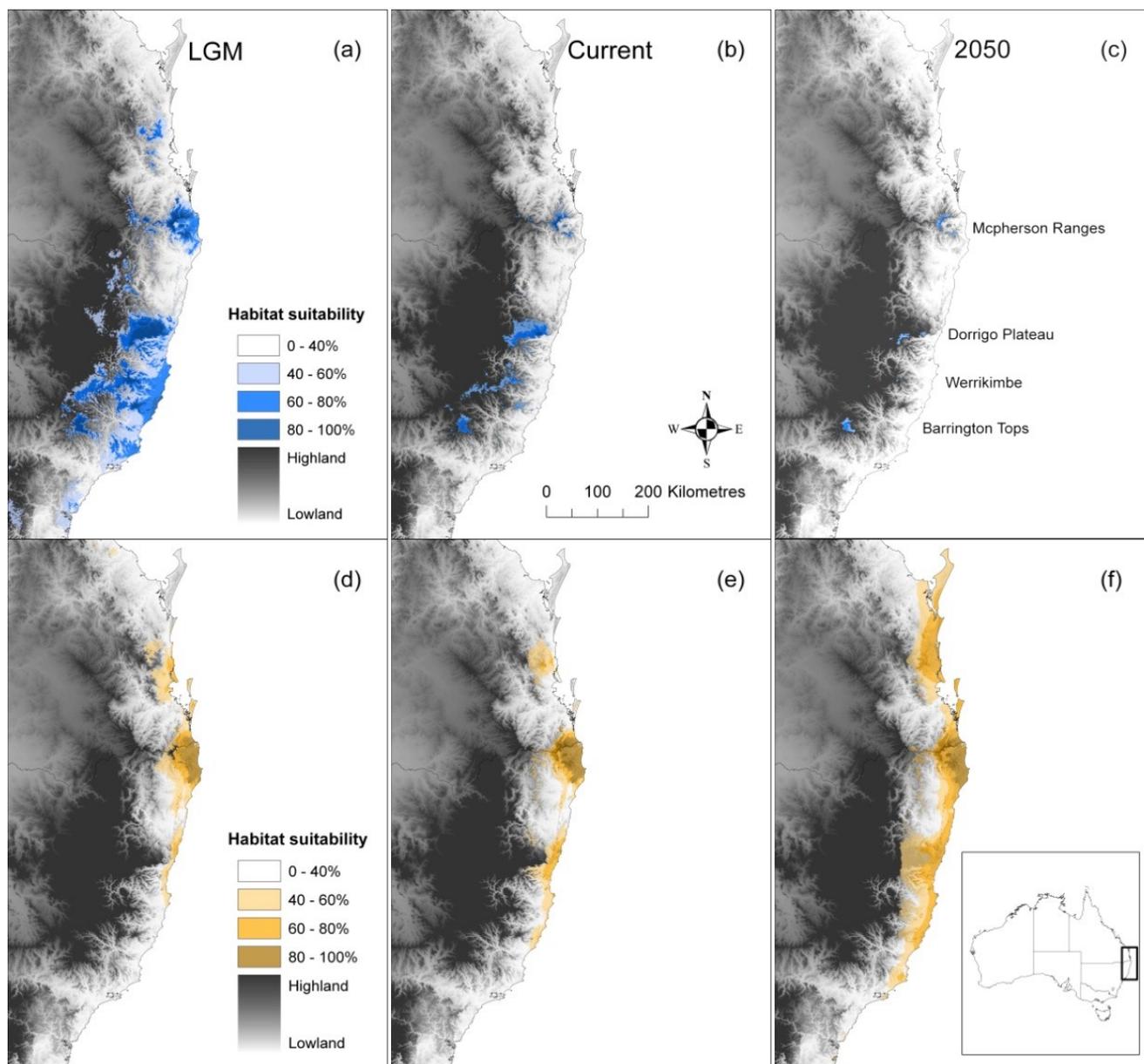
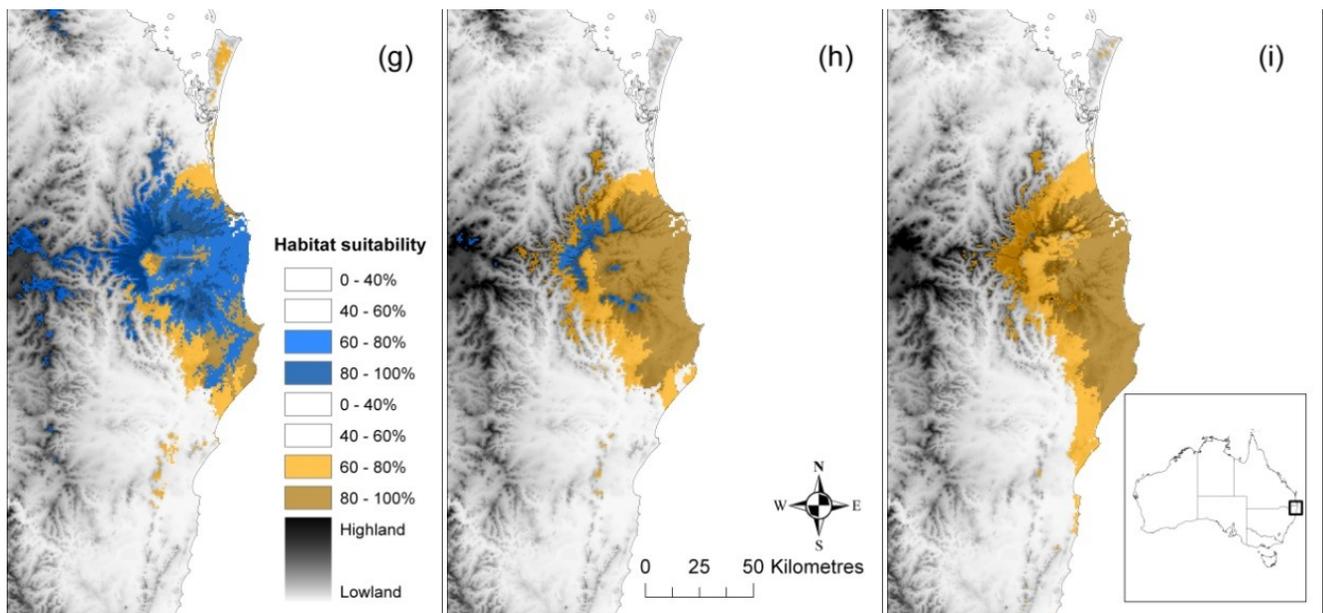


Figure 1. Cont.



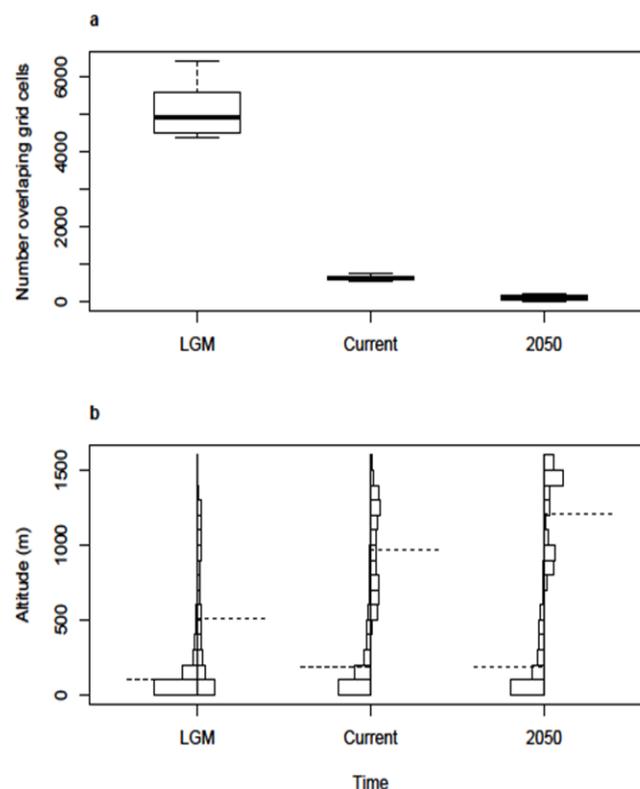
2.2. Spatial and Altitudinal Overlap

Analysis of area of overlap for *Nothofagus moorei* and *Elaeocarpus grandis* for each time shows the maximum overlap between the two models occurred during the LGM and was mostly a consequence of the down-slope movement of the envelope for *N. moorei* (Figure 2a). Histograms of frequency of altitude values in the core climate condition grid cells for each species (Figure 2b) show that the average elevation of *E. grandis* occurrences has increased 100 m in elevation since the LGM, while the average elevation of *N. moorei* occurrences has increased 500 m since the LGM, and is predicted to increase another 200 m by 2050.

2.3. Discussion

The models show a continuing contraction of the highland cool temperate climatic envelope and expansion of the lowland warm subtropical envelope, with both showing upslope shifts in response to post-glacial warming. Distributional changes in response to climate offer insight into the impact of selective filters upon species-specific traits and potentially explain why species/community associations persist under dramatic environmental change. Species such as *Elaeocarpus grandis* that are adapted to warmer conditions (e.g., tropical lowlands) are likely to differ in a broad range of traits from *Nothofagus* species, which typify the uppermost canopy of montane cool temperate rainforests [21].

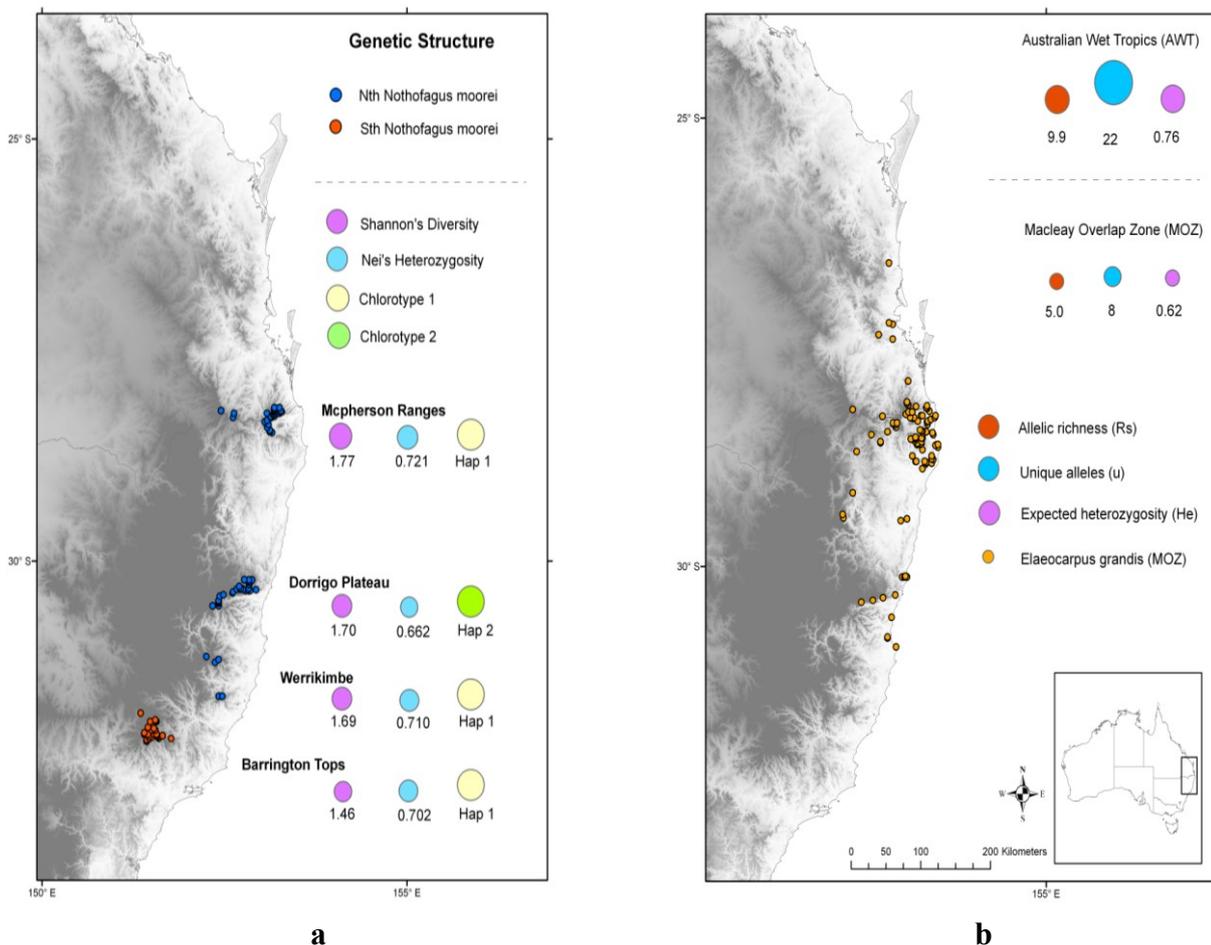
Figure 2. (a) Analysis of area of overlap and altitudinal distribution for *Nothofagus moorei* and *Elaeocarpus grandis*. Boxplots of area of overlap at each time for 10 paired replicate models. Area of overlap was measured as number of overlapping grid cells marked as core climate conditions for each species; (b) Histograms of frequency of altitude values in the core climate condition grid cells for each species. *Elaeocarpus grandis* data is to the left and *N. moorei* to the right in each panel. Histograms of altitude in 100 m bands were based on the core climate suitability grid cells for each species pooled across the 10 replicates at each time. The dashed line on each plot indicates the mean altitude for each species.



We summarised genetic data obtained from existing literature to find that the overall genetic diversity of *Nothofagus moorei* populations (*i.e.*, Shannon's Diversity Index, $I = 0.2719$; and Nei's Gene Diversity, $h = 0.1672$) was relatively high compared to other temperate rainforest trees [30,31]. Taylor *et al.* [31] found little evidence of clonality outside multi-stemmed rings of each individual, and observed genetic diversity was considerably higher in the northern (McPherson Ranges, Shannon's Diversity = 1.77; Nei's Heterozygosity = 0.721) than in the southern range (Barrington Tops, Shannon's Diversity = 1.46; Nei's Heterozygosity = 0.702) (Figure 3a). Furthermore, genetic differentiation was significantly positively correlated with geographic distance in areas of higher diversity but not in areas of lower diversity [30,31]. The majority of genetic variation was partitioned among individuals within population (60%; $p < 0.001$), rather than among populations within regions (10%; $p < 0.001$), yet a large and significant component of the measured diversity was partitioned between northern and southern regions (29%; $p < 0.001$) [31].

Schultz’s thesis [30] showed the maternally inherited chloroplast genome amplified only two haplotypes, with the Dorrigo population in the centre of the range having a unique haplotypic variant different from all other populations (Figure 3a). Pairwise population differentiation and genetic structure analyses suggest ancestral distinction between these population groups has been maintained in the presence of gene flow, however high pairwise differentiation was measured between Barrington Tops and all other sites [30].

Figure 3. (a) The entire (northern and southern) *Nothofagus moorei* occurrences (YETI and Atlas of NSW Wildlife), including genetic structure [31] and diversity [30,31] across whole range, that comprises four major highland population groups. Areas of higher elevation are indicated by darker shading and areas of lower elevation are indicated by lighter shading; (b) The *Elaeocarpus grandis* occurrences (YETI and Atlas of NSW Wildlife) and genetic diversity of the southern Macleay Overlap Zone [33] and the northern Australian Wet Tropics occurrences [42].



High genetic diversity of *E. grandis* is reflective of the range it occupies, yet the absence of significant structure (Figure 3b) suggests its dispersal ability and potential to migrate accounting for its extensive distribution also maintains between population connectivity [33,42,43]. Overall levels of genetic diversity (*i.e.*, allelic richness, $R_s = 5$ and expected heterozygosity, $H_e = 0.62$) (Figure 3b) were higher than those of closely related endemic species, yet lower than those recorded for other woody rainforest taxa [33].

The observed genetic structure among population groups of *N. moorei* (Figure 3a) suggests sensitivity to abiotic pressures and poor dispersal ability across the landscape-level barriers separating suitable habitat caused genetic drift and divergence. Although the models suggest current climatic conditions are suitable for expansion into adjacent areas, the effects of fire and floristic competition most likely prohibit establishment in new areas. The models show *N. moorei* will potentially reach an environmental ceiling by 2050 (Figure 1i: The Lamington and Border Ranges National Parks altitudinal limits). The variable contribution of the *N. moorei* model indicates precipitation is the major determinant of the current distribution, yet mean temperature of the warmest quarter (7%) and maximum temperature of the driest month (7%) also contributed to the model generated.

Competitive exclusion from lower elevations may restrict the current distribution to areas of relatively lower alpha diversity. The species is known to disperse from established population higher in the catchment into lower elevations along rivers but these populations are not known to establish [30]. Extreme fire events and the exclusion by fast-growing rainforest or fire-adapted elements are likely to contribute to this limitation on the current distribution. In the absence of fire and competition, the species would be capable and likely to colonise lower elevations.

While also restricted by fire, *E. grandis* is frost-sensitive and limited by low temperatures, making the species physiologically incapable of colonising highland areas. As the increase in temperature predicted for 2050 can shift this physiological barrier upwards, altitudinal limitations in distribution for *E. grandis* might be removed (Figure 1f,i). *Elaeocarpus grandis* is an efficient disperser and rapid expansion into newly available habitat is potentially achievable [33].

Assuming *N. moorei* will persist in habitat of low-climatic suitability, as it has for long periods in the past; it is likely that (in the absence of extreme fire events) co-occurrence of *E. grandis* and *N. moorei* may arise in the future. This could potentially lead to a sub-tropical taxa insurgency into higher elevations and some displacement, yet various long-lived temperate elements are likely to remain as they have in the past. In the absence of extreme fire events, cloud forests may persist yet floristically change to include elements of lowland forests. However, it is important to note that as suggested by our LGM models (Figure 1a–c) and by palaeoecological studies [13], overlaps and assemblage reshuffles have occurred in the past. For instance, a number of frost-sensitive subtropical species might have been selectively filtered against at lower elevations during the cooler conditions of the glacial peaks, while cool adapted lineages capable of dispersing could have expanded their distributional range into lower elevations.

The broad latitudinal gradients of intra-specific diversity in rainforest species [5,6] emphasise the idea that in fragmented distributions, observed genetic diversity is a product of local (endemic) processes and dispersal events. The molecular history of populations is therefore dependent in a complex way upon species traits related to dispersal and physiological tolerances which determine a species' fundamental niche. Furthermore, the findings emphasise that climate, although a major determinant of a species' range or observed distribution, is only one facet of many that defines a species' niche and therefore its potential distribution.

3. Experimental Section

Climate envelope modelling was used to predict the historical geographic range and infer past contraction and expansion events of a highland (*Nothofagus moorei*) and a lowland (*Elaeocarpus grandis*) species. Occurrence records (109 for *N. moorei* and 105 for *E. grandis*) were compiled and verified from the Office of Environment and Heritage's vegetation survey database (YETI) [44] and Atlas of Living Australia [45] databases.

Observed climate of the late 20th Century was provided by the WorldClim 1.4 data [46] at 30 arc second resolution, referred to hereon as "current climate". We used all 19 original bioclimatic variables [47], which are provided in the WorldClim data set. Models for each species were trained on current climate, and projected onto estimated climate at the last glacial maximum (LGM). For these climate data we used the MIROC 3.2.2 medium resolution global climate model (GCM) available from the PMIP2 website [48].

To account for uncertainties in predictions of future climate data, we derived data from 13 global climate models (GCMs) used in the Fourth Assessment Report of the Inter-governmental Panel on Climate Change (IPCC) [49], which provided the raw temperature and precipitation variables needed to compute the derived bioclimatic variables used to fit the climate envelope models. We chose GCM model runs for the A2 greenhouse gas scenario [50] because assessments of observed trends in greenhouse gas levels suggest that this scenario closely matches the observed trends [51]. Raw GCM data for the decade centered on 2050 was obtained from the Climate Model Inter-comparison Project dataset [52].

A custom-written program as used to downscale the coarsely-gridded GCM data for both LGM and future climates using bicubic spline interpolation [53] to the same 30 arc second grid as the WorldClim data. We then computed the 19 bioclim variables for each GCM also using a custom-written program.

Model training on current climate data, and projection onto LGM and 2050 climates, was performed using MAXENT 3.3.3e [54,55]. The machine-learning maximum entropy application, MAXENT has been shown to consistently outperform other modelling methods when generating models of the relationship between environment and species occurrence [56,57]. MAXENT is based on a probabilistic structure that relies on the hypothesis that the incomplete observed probability distribution (based on occurrence data) can be approximated with a probability distribution of maximum entropy to a species' potential geographic distribution [54,58,59], that is associated with the species' realised niche. We refined the current model using methodology described in Mellick *et al.* [5,6].

The lower LGM sea level was not included in the model projections because the areas of interest (*i.e.*, areas of inferred community turn-over) to the study are mountainous rather than coastal areas that otherwise would necessitate lowered bathymetry.

The extent of core or most favourable climate conditions for each species was determined by producing binary (presence-absence) maps of the MAXENT output maps using the values for "equal test sensitivity and specificity logistic threshold" provided by MAXENT. This threshold has been demonstrated to have good statistical properties [59]. However, the use of this threshold produced maps of high suitability that were too broad to be interpreted biologically as they included large areas where each species does not occur. In part, this reflected the fact that we have produced climate

suitability models which do not incorporate a number of other important factors likely to influence the distribution of each species (e.g., competition, fire, orographic uplift).

We used the following method to identify core areas of climate suitability. Using the replicate threshold maps for each species described above, we identified those grid cells marked as suitable by all 10 replicate models. We interpreted this area as core habitat. For each model replicate for each species, we found the minimum MAXENT logistic-scale climate suitability score within the core area. These values were used to re-threshold the current climate maps for each species to provide binary maps of the biologically conservative areas of suitability. The set of thresholds was also applied to the replicate maps for LGM and 2050 projections of the models.

Using the re-threshold maps, we calculated the number of cells that overlap between each species paired replicate maps at each time step (Figure 2a). That is, we calculated the overlap between replicate 1 for *N. moorei* and replicate 1 for *E. grandis* at the LGM, and so on for the 10 LGM replicates, repeating these calculations for current climate and 2050 map sets.

To understand the altitudinal distribution of each species at each time we created histograms of the number of grid cells falling into 100 meter bands for each species at each time by pooling the altitude of each occupied grid cell for all 10 replicate models (Figure 2b). The altitude data we used was at 30 arc second resolution (approximately 1 km grid cells) and was downloaded from the WorldClim website [60].

We used version 2.15 of the R statistical environment [61] to perform all threshold and altitude distribution computations.

4. Conclusion

The climate envelope models suggest the distribution and genetic diversity/structure in *Nothofagus moorei* and *Elaeocarpus grandis* are a result of species-specific functional and ecological strategies in the context of the abiotic limitations of their environment. The spatial extent of climate suitability for 2050 (Figure 1) suggests a continued contraction of current *N. moorei* climatic envelope, and an opposing trend for *E. grandis*. Current altitudinal differences between *N. moorei* and *E. grandis* are likely to be a result of contrasting evolutionary strategies. *Elaeocarpus grandis* shows a pioneering strategy with emphasis on colonisation of new habitats (e.g., attractive fruit, early-succession and fast growth), while *N. moorei* shows a persistence strategy (e.g., pollen dispersal, coppicing and extremely long life cycle). The absence of *N. moorei* from areas of high habitat suitability [30] is a likely reflection of a combination of factors such as fire sensitivity, poor dispersal ability and shade intolerance. Thus *N. moorei*, and the unique cool temperate alliance found within the microhabitats provided by its trunk [25] are potentially more vulnerable to anthropogenic climate change than the more widespread *E. grandis*. Although *Nothofagus* has been exposed to extreme climate change before, the geologically recent loss of the lineage from the Australian Wet Tropics [62] serves as a warning.

Acknowledgements

The authors thank The Royal Botanic Gardens and Domain Trust, Sydney, and, Macquarie University, Sydney.

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