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Temperature, nutrient availability, and species traits interact to shape elevation responses of Australian tropical trees

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Elevation gradients provide natural laboratories for investigating tropical tree ecophysiology in the context of climate warming. Previously observed trends with increasing elevation include decreasing stem diameter growth rates (GR), increasing leaf mass per area (LMA), higher root-to-shoot ratios (R:S), increasing leaf $\delta^{13}\text{C}$, and decreasing leaf $\delta^{15}\text{N}$. These patterns could be driven by decreases in temperature, lower soil nutrient availability, changes in species composition, or a combination thereof. We investigated whether these patterns hold within the genus *Flindersia* (Rutaceae) along an elevation gradient (0–1,600 m) in the Australian Wet Tropics. *Flindersia* species are relatively abundant and are important contributors to biomass in these forests. Next, we conducted a glasshouse experiment to better understand the effects of temperature, soil nutrient availability, and species on growth, biomass allocation, and leaf isotopic composition. In the field, GR and $\delta^{15}\text{N}$ decreased, whereas LMA and $\delta^{13}\text{C}$ increased with elevation, consistent with observations on other continents. Soil C:N ratio also increased and soil $\delta^{15}\text{N}$ decreased with increasing elevation, consistent with decreasing nutrient availability. In the glasshouse, relative growth rates (RGR) of the two lowland *Flindersia* species responded more strongly to temperature than did those of the two upland species. Interestingly, leaf $\delta^{13}\text{C}$ displayed an opposite relationship with temperature in the glasshouse compared with that observed in the field, indicating the importance of covarying drivers in the field. Leaf $\delta^{15}\text{N}$ increased in nutrient-rich compared to nutrient-poor soil in the glasshouse, like the trend in the field. There was a significant interaction for $\delta^{15}\text{N}$ between temperature and species; upland species showed a steeper increase in leaf $\delta^{15}\text{N}$ with temperature than lowland species. This could indicate more flexibility in nitrogen acquisition in lowland compared to upland species with warming. The distinguishing feature of a mountaintop restricted *Flindersia* species in the glasshouse was a very high R:S ratio in nutrient-poor soil at low temperatures, conditions approximating

the mountaintop environment. Our results suggest that species traits interact with temperature and nutrient availability to drive observed elevation patterns. Capturing this complexity in models will be challenging but is important for making realistic predictions of tropical tree responses to global warming.

KEYWORDS

elevation gradient, *Flindersia*, growth temperature, leaf $\delta^{13}\text{C}$, leaf $\delta^{15}\text{N}$, relative growth rate, root-to-shoot ratio, soil nutrient availability

1. Introduction

Elevation gradients, and their associated changes in temperature, provide natural laboratories for studying how tropical trees might respond to global warming (Malhi et al., 2010; Tito et al., 2020). Increasing elevation, and by extension lower temperatures, have been associated with both species-specific and community-based trends; these include decreasing growth rates (Rapp et al., 2012), increasing root-to-shoot ratios (R:S) (Fahey et al., 2016), increasing leaf mass per area (LMA) (Rapp et al., 2012; Van De Weg et al., 2012; Fahey et al., 2016), increasing foliar $\delta^{13}\text{C}$, and decreasing foliar $\delta^{15}\text{N}$ (Sparks and Ehleringer, 1997; Li et al., 2009). Foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been used as indicators of intrinsic water-use efficiency (Cernusak et al., 2013), and ecosystem nitrogen cycling (Martinelli et al., 1999), respectively. However, although some of these trends with increasing elevation appear to be general in the literature (Vitousek et al., 1990; Bauters et al., 2017; Mumbanza et al., 2021), the mechanisms driving the observations are not fully resolved. Disentangling the direct and indirect role that temperature plays in determining these trends in plant functional traits is vital to understanding elevation gradients as proxies for predicting the response of forests to future climate scenarios.

In addition to decreasing temperatures, increasing elevation is associated with variation in other climatic factors, such as precipitation, vapor pressure deficit, and solar radiation (Malhi et al., 2010). Similarly, the availability of soil nutrients, such as N and P, can also change as a function of elevation, both because of changes in temperature-driven mineralization rates, and inherent litter decomposability (Salinas et al., 2011). Together, these environmental factors are all recognized as major drivers of tropical tree growth and selective filters for plant functional traits (Rapp et al., 2012; Cheesman et al., 2018; Bauman et al., 2022a). Trends in functional traits observed across elevation may therefore result from, to varying degrees, changes in temperature, vapor pressure deficit, soil nutrients, species turnover, and the interaction of these factors (Read et al., 2014; Fahey et al., 2016).

Declining temperatures and nutrient availability with increasing elevation can influence resource allocation in tropical trees (Unger et al., 2012). For example, N allocation toward photosynthetic tissues may be reduced (Xiao et al., 2018; Ziegler et al., 2020), and climatic and soil conditions may favor biomass allocation toward roots (Kobe et al., 2010; Poorter et al., 2012). This may lead to the selection of species at high elevations with functional adaptations for slower growth, such as an intrinsically high R:S, and with leaf traits oriented toward the slow end of the leaf economic spectrum, including a larger leaf mass per unit leaf area (LMA), lower mass based N concentration, and a more robust leaf structure associated with longer leaf lifespans

(Wright et al., 2005; Valladares and Niinemets, 2008; Poorter et al., 2012). Low temperatures and nutrient availability may also lead to the production of leaves, leaf-litter, and thereby soil organic material with limited N availability and a highly recalcitrant carbon content. This self-reinforcing trend may lead to observed traits being directly impacted by nutrient availability and decoupled (in the short term) from the direct impacts of changing temperature.

The relationship between water availability and foliar $\delta^{13}\text{C}$ is generally well-established (Diefendorf et al., 2010), with foliar $\delta^{13}\text{C}$ becoming more negative as precipitation and soil water availability increase. Yet, somewhat surprisingly, leaf $\delta^{13}\text{C}$ often becomes higher with elevation in spite of general increases in water availability (Sparks and Ehleringer, 1997); this appears to be related to increasing LMA and decreasing atmospheric pressure (Körner, 2007; Chen et al., 2017). Higher LMA can increase the leaf internal resistance to CO_2 diffusion, thereby reducing chloroplastic CO_2 concentrations during photosynthesis (Cernusak et al., 2013), resulting in an increase in the foliar $\delta^{13}\text{C}$ (Vitousek et al., 1990; Li et al., 2009). Increased LMA can also lead to increased leaf N and P concentrations per unit leaf area, which can confer increased leaf photosynthetic capacity, further decreasing discrimination against ^{13}C (Bauman et al., 2022a). Nevertheless, decreases in foliar $\delta^{13}\text{C}$ with increasing elevation have been reported in some cases (Sah and Brumme, 2003), and could be related to lower leaf-to-air vapour pressure deficits (VPD) with increasing elevation, resulting in an increased ratio of intercellular to ambient CO_2 concentrations (c_i/c_a) through opening of stomata (Cernusak et al., 2013; Chen et al., 2017).

Foliar $\delta^{15}\text{N}$ has been observed to decrease with increasing elevation in tropical rainforest trees (Bauters et al., 2017). This is thought to be the result of more open N cycling at warm, low elevations, and with tighter N cycling at higher elevations as a result of slower N mineralization rates caused by low temperatures and less decomposable litter (Martinelli et al., 1999; Baumgartner et al., 2021). More open N cycling feeds N loss pathways from the ecosystem that tend to leave the residual N pool relatively enriched in ^{15}N (Martinelli et al., 1999; Craine et al., 2015). Some studies have also reported a positive trend or no change in foliar $\delta^{15}\text{N}$ with elevation, attributing this to increased water stress in some mountainous regions, or due to the nature of site-specific biogeochemical processes; such as ammonium immobilization for example (Vitousek et al., 1989; Yi and Yang, 2006). Likewise, differences in plant functional types are known to contribute toward variation in foliar $\delta^{15}\text{N}$ due to differences in nitrogen acquisition strategies and microbial associations, such as symbiotic associations with N fixing bacteria and mycorrhizal fungi (Cernusak et al., 2009; Liu et al., 2010). However, within species from a single genus found in moist tropical rainforests, we would not expect to find these latter complications. Thus, $\delta^{15}\text{N}$ signatures

can still be generally useful as indicators of nitrogen cycling at the ecosystem scale and across environmental gradients, if care is taken to minimize variation associated with different plant functional types and ecological strategies (Amundson et al., 2003).

Understanding how temperature directly and indirectly shapes observed patterns in species distribution and plant functional traits across elevation will allow a mechanistic understanding of how changing temperatures are likely to impact natural systems. In this study, we first examined patterns of tree stem diameter growth and leaf functional traits (LMA, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in a dominant tropical rainforest tree genus, *Flindersia*, distributed along an elevation gradient in the Australian Wet Tropics World Heritage Area (Bradford et al., 2014a). We then conducted a glasshouse experiment to examine the relative impacts of temperature, soil nutrient availability, and species in driving these observations. We hypothesized that trends across elevation would reflect a combination of both direct temperature effects, indirect temperature effects mediated by nutrient availability, and species' traits associated with habitat preference (lowland versus upland). To gain insight, we used the glasshouse experiment to test for effects of temperature and nutrient availability, and their interactions with species and habitat preference, on growth rates, biomass allocation, LMA, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

2. Materials and methods

2.1. Species selection and study area

Flindersia R.Br., of the family Rutaceae, comprises ca 17 species of trees and shrubs distributed across Malesia, Australia, and New Caledonia, with 15 species known to occur in the tropics and subtropics of Australia (Scott et al., 2000; Bayly et al., 2013). Nine species in the Australian Wet Tropics are commonly observed among the dominant taxa and contribute to biomass in rainforest plots in these forests (Bradford et al., 2014a), ranging from near sea level to the summits of the highest peaks (Zich et al., 2020). *Flindersia*, in general, are known to reliably produce seeds, which are enclosed in fruits that are easy to spot in the canopy, and are therefore more accessible compared to seeds of some other co-occurring taxa (Zich et al., 2020). We explored herbarium records and species distribution observations from the Atlas of Living Australia (ALA) (Belbin, 2011) and used these observations to identify four focal *Flindersia* species for this study: *F. iffiana* F. Muell., *F. bourjotiana* F. Muell., *F. brayleyana* F. Muell., and *F. oppositifolia* (F. Muell.) T.G. Hartley & L.W. Jessup. *Flindersia oppositifolia* is a tropical mountaintop species with a very restricted distribution and a narrow climate niche, whereas the other species are more widely distributed along the elevation gradient and have a broad climate niche. Among these, *F. brayleyana* displays a predominantly upland distribution, whereas *F. bourjotiana* and *F. iffiana* have predominantly lowland distributions (Supplementary Table 1).

We filtered the ALA observations for each species using the spatial thinning package 'spThin' (Aiello-Lammens et al., 2015) in R, set at a scale of 0.5 km for the mountaintop restricted species and 5km resolution for the widespread taxa at 10 repetitions for each species, which returned a total of 95 spatially-thinned occurrences within the Australian Wet Tropics. We then extracted a suite of gridded environmental variables from WorldClim for the occurrence locations, including mean annual temperature (BIO1) (Figure 1A)

and mean annual precipitation (BIO12) (Figure 1B; Fick and Hijmans, 2017).

2.2. Stem diameter growth and plant functional trait measurements across elevation

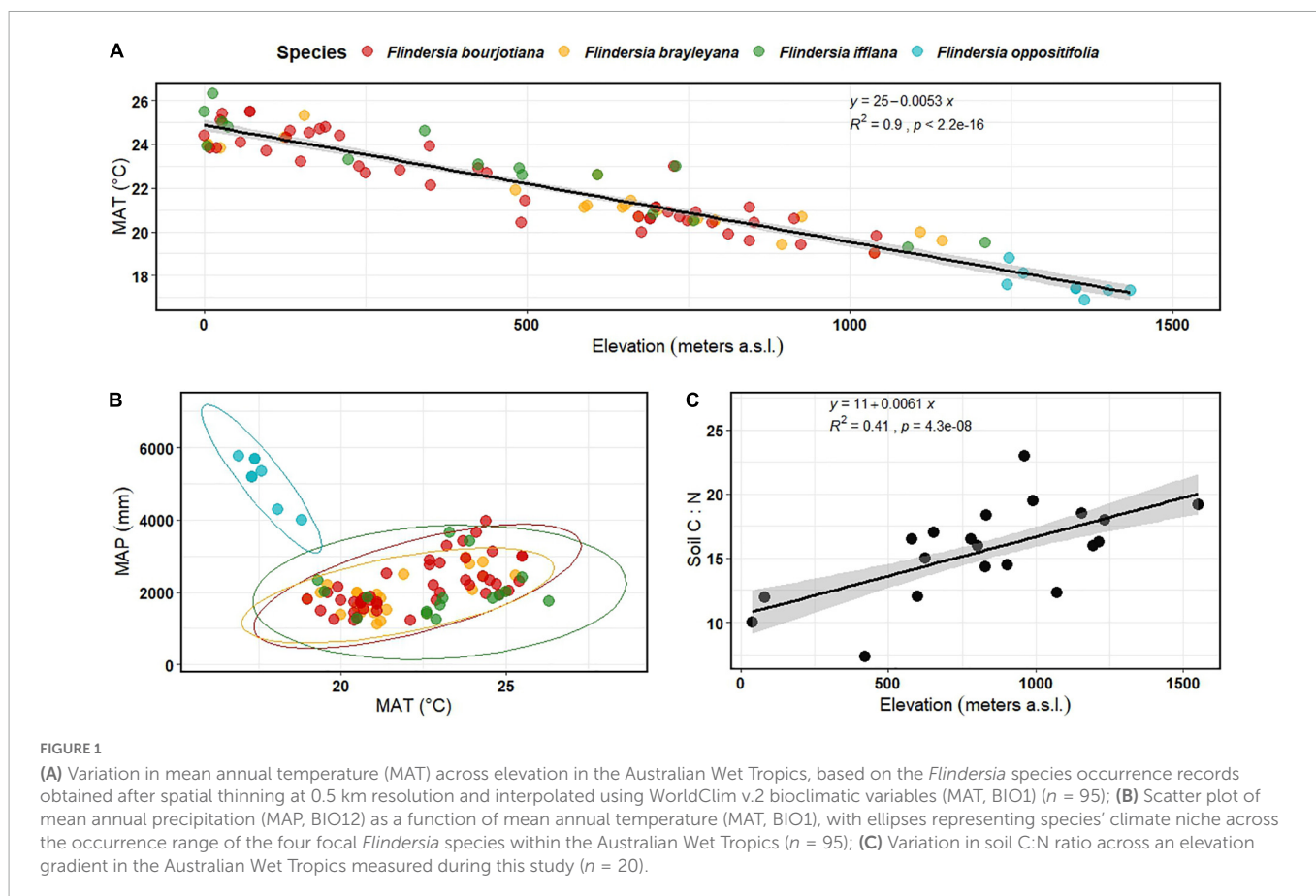
Individual stem diameter growth rates (GR) were calculated for mature rainforest *Flindersia* species distributed across elevation in the Australian Wet Tropics and captured in long-term forest census plots ($n = 13$ sites). For each individual within a site, we calculated the linear increase in diameter for stems greater than 10 cm diameter at breast height ($n = 2$ to 20 individuals per site) between 1971 and 2013 (Bradford et al., 2014b). For *F. oppositifolia*, restricted to mountaintops, we calculated GR ($n = 33$ individuals) for the period from 2010 to 2019 using a rainforest plot established by Torello Raventos (2014), which we re-censused in 2019. Field campaigns to collect plant functional traits (LMA, foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of exposed canopy branches of focal *Flindersia* species (a minimum of 2 individuals per site) were conducted in four locations (Supplementary Table 1) across a range in elevation, using standard trait measurement protocols (Cornelissen et al., 2003). Data from a previous trait campaign (Bauman et al., 2022a) were also added to this analysis ($n = 16$ individuals across five sites for the focal species).

2.3. Soil nutrient and isotope analyses across elevation

Surface soil samples were collected from 20 rainforest plots spanning an elevation range from 40 to 1,550 m in the Australian Wet Tropics. Of these, 16 plots had dimensions 20 m \times 20 m, whereas the mountaintop plot had dimension 50 m \times 20 m, and the two lowland sites were each 100 m \times 100 m. The sites were selected to include those for which soils were derived from granitic parent material, except for the two lowest elevation plots, for which soils were derived from granitic and metamorphic colluvium. Five cores per site (at the 4 corners of the plot and one at the center) were sampled using an auger (~10 cm deep) after removing leaf litter. Samples were bulked and homogenized at the plot level. Samples were then oven-dried at ~105°C for 72 h and ground to a fine powder using a Benchtop Ring Mill (Rocklabs, Mineral Stats INC., Colorado) at the Advanced Analytical Centre (AAC), James Cook University (JCU), Cairns. Soil pH in H₂O and in 0.01M CaCl₂ was measured on oven-dried samples using an ISFET pH pen (Model 24006 DeltaTrak). Subsamples were used to determine C and N concentrations and isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as described below for leaf tissue. Total soil P was analyzed using a microwave assisted acid digestion of oven dried samples followed by ionization detection using the Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES) at the AAC, JCU, Townsville.

2.4. Glasshouse experimental growth conditions

We collected seeds from the four focal species, with each species collected at a single site (Supplementary Table 1). The



four collection sites were distributed across most of the elevation range found in the Australian Wet Tropics (Lowland species, *F. ifflana* ~ 300 m and *F. bourjotiana* ~ 600 m, and Upland species *F. brayleyana* ~ 990 m and *F. oppositifolia* ~ 1,550 m). The seeds were allowed to germinate under ambient shade-house conditions at the Environmental Research Complex (ERC), (~30 m a.s.l.) JCU, Cairns, Australia. Healthy saplings were transplanted (approximately 3 months after sowing seeds) into either 13.5 L pots (Garden City Pots, Model: P300ST00) containing nutrient-rich soil (NR), comprising a 1:1 mixture by volume of premium garden potting mix and compost (Northside Landscape Supplies Pty. Ltd., Trinity Beach); or 8.5 L pots (Garden City Pots, Model: P250STTL) containing nutrient-poor soil (NP). The nutrient-poor soil comprised a locally collected dermasol, low in organic matter and supplemented with perlite and washed river sand to improve drainage (Supplementary Table 2). The two soil mixtures, nutrient-rich and nutrient-poor, had similar $\delta^{15}\text{N}$ at the start of the experiment, based on measurements of subsamples; these values were 5.4 and 5.3‰, respectively.

The experimental pots were transferred into a climate-controlled glasshouse facility. The facility is divided into three temperature-controlled chambers, each with a shade screen (SOLARO, Ludvig Svensson Inc. Kinna, Sweden) that reduces incident irradiance to approximately 50% of the incoming irradiance. Further details of the experimental facility can be found in Forbes et al. (2020). Three growth temperature treatments were implemented by setting chambers to track the external temperature profile with a chamber-specific offset, specifically a) 0°C offset, b) -7°C offset, and c) +5°C offset. These chamber temperature conditions mimic the lowland

provenance, mountaintop provenance, and a lowland warming scenario, respectively. The climatic conditions were controlled via the Building Management System (BMS) with temperature and relative humidity (RH) in each chamber measured (QFM2160 Temperature and Humidity Probe, Siemens) and recorded at 5 min intervals in the BMS. We further characterized the temperature regimes with a Temperature Soil Moisture Sensor [TMS-4, TOMST s.r.o, Prague, (Wild et al., 2019)] in each experimental chamber to record the temperature in the immediate environment of the saplings. A summary of chamber conditions over the course of the experiment is given in Table 1. We calculated the VPD of each chamber from the temperature and relative humidity measurements (Campbell and Norman, 1998).

A minimum of three healthy saplings per soil treatment per species were monitored for growth in each chamber to give a total of 24 saplings (3 Saplings \times 2 Soil treatments \times 4 Species) per chamber. All pots were hand-watered to field capacity daily throughout the experiment. To avoid any chamber bias across the experimental treatments, the treatments were rotated among the chambers monthly.

2.5. Glasshouse experimental biomass measurements

Before the start of the glasshouse experimental treatments, initial plant biomass was estimated for individuals using a species-specific allometric relationship derived from root-collar diameter, stem height, and the total dry biomass of three destructively harvested

TABLE 1 Environmental conditions in the glasshouse during the experiment for the three glasshouse chambers.

Time	Cold				Ambient				Elevated			
	Temperature (°C)		RH (%)	VPD (kPa)	Temperature (°C)		RH (%)	VPD (kPa)	Temperature (°C)		RH (%)	VPD (kPa)
	BMS	TOMST			BMS	TOMST			BMS	TOMST		
Day	19 ± 3.2	17 ± 3.5	76 ± 5.8	0.53 ± 0.24	26 ± 3.6	25 ± 3.5	83 ± 8.5	0.61 ± 0.37	31 ± 4.1	30 ± 4.6	71 ± 11	1.39 ± 0.69
Night	14 ± 1.9	12 ± 1.9	84 ± 3.5	0.26 ± 0.08	20 ± 3.1	19 ± 3.1	91 ± 6.3	0.22 ± 0.18	25 ± 3.1	24 ± 3.1	79 ± 9	0.68 ± 0.36
Average	16.5 ± 2.5	14.5 ± 2.7	80 ± 4.6	0.40 ± 0.16	23 ± 3.35	22 ± 3.3	87 ± 7.4	0.41 ± 0.27	28 ± 3.6	27 ± 3.8	75 ± 10	1.03 ± 0.52

Air temperature was recorded using the building management system (BMS) software and additionally with a temperature moisture sensor (TMS-4, TOMST, Czech Republic), recorded at intervals of 5 min. Relative humidity (RH) and vapor pressure deficit (VPD) were recorded with the BMS. All values given in means ± 1SD. Daytime and night-time have been separated, with daytime being hours between 0700 and 1700 local time.

saplings. Final biomass was measured from destructive harvests of three plants per species by treatment combination, except for *F. bourjotiana* in the nutrient-rich, elevated temperature treatment, where only two plants survived. Thus, a total of 71 plants were harvested for final biomass.

The dry mass of leaves, stems and roots were measured separately and used to calculate Above Ground Biomass (AGB, sum of leaf and stem dry mass) and Below Ground Biomass (BGB, total root dry mass). The AGB and BGB were used to calculate the root-to-shoot ratio (R:S). From each plant, three to four leaves were collected for determination of LMA, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, as described below. Relative growth rates (RGR, $\text{mg g}^{-1} \text{day}^{-1}$) were calculated using equation 1 (Hoffmann and Poorter, 2002):

$$\text{RGR} = \frac{\ln(M_f) - \ln(M_i)}{\Delta t} \quad (1)$$

where, M_f is the final biomass, M_i is the estimated initial biomass, and Δt is the length of the experiment in days.

2.6. Leaf-level functional traits

For both field-collected, and glasshouse grown leaves, leaf area was calculated from scanned fresh leaves (3 to 5 leaves per individual) using Image-J software, which in conjunction with oven-dried leaf mass was used to calculate LMA (g m^{-2}). Further, oven-dried leaves were ground to a fine powder using a Bench Top Ring Mill. Foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios were determined using a Costech Elemental Analyzer, fitted with a zero-blank auto-sampler and coupled via a ConFloIV interface to a Thermo Finnigan Delta-V PLUS isotope ratio mass spectrometer (Bremen, Germany). Stable isotope results are reported as per mil (‰) deviations from the VPDB and AIR reference standard scales for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Precisions (± 1 standard deviation) on internal standards were better than $\pm 0.1\text{‰}$ and $\pm 0.2\text{‰}$ for C and N, respectively.

2.7. Statistical analysis

2.7.1. Field observations

All statistical analyses were conducted within the 'R studio' environment, using R version 4.1.2 (R Core Team, 2021). We computed ordinary least-squares linear regressions for each of the response variables to understand how field observed traits (i.e., GR, LMA, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) varied with elevation

(Supplementary Table 3). We conducted these analyses at the genus level; that is, individual species identities were not accounted for in the models. For the field measurements, each species was sampled at one or few locations, and so accounting for individual species did not improve the models. All dependent variables were checked for normality assumptions using the Shapiro–Wilk's test for normality and we used square root transformation on GR to meet normality assumptions. Predictor variables were standardized prior to analyses. The 95% Confidence Intervals and *P*-values were computed using the Wald approximation.

2.7.2. Glasshouse experiment

We computed ordinary least-squares linear regressions for each of the response variables: RGR, R:S, LMA and foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ against Temperature, Soil nutrient status (i.e., nutrient-rich versus nutrient-poor), Species and the interactions between Species and Temperature and Soil nutrient status. Model selection was carried out using the 'performance' package in R (Lüdecke et al., 2021), and the model that yielded the lowest AIC was then chosen for each of the response variables. Temperature was taken as a continuous variable from the long-term air temperature averages for each growth chamber (Table 1). Type III ANOVA was performed on the chosen models, followed by *post hoc* comparisons of means using the 'emmeans' package in R (Lenth et al., 2018). We built a custom linear contrast for comparison of species according to their habitat preference (lowland versus upland), for response variables where Species interacted with Temperature. We did this to better understand whether species responses were structured by their elevation preference. For this comparison *F. ifflana* and *F. bourjotiana* were considered as lowland, and *F. brayleyana* and *F. oppositifolia* as upland. We checked for normality using visual histograms on all dependent variables, and then a Shapiro–Wilk's test for normality was performed followed by testing the homogeneity of variances ($P > 0.05$). We log-transformed the response variables RGR and used square root transformation for LMA to meet normality assumptions.

3. Results

3.1. Field observations: Temperature and soil nutrient availability with elevation

Recorded observations of the four focal *Flindersia* species in the Australian Wet Tropics, in conjunction with gridded climate data for each observation location, indicated a linear decline in Mean Annual

Temperature (MAT) with elevation in the distribution ranges, with a slope of $-5.3^{\circ}\text{C km}^{-1}$ (Figure 1A). The three widespread species shared similar climate niche space (based on its MAT and Mean Annual Precipitation (MAP)), while the mountaintop-restricted species displayed the lowest MAT and highest MAP (Figure 1B; Supplementary Table 1). Further, for the three widespread species, elevational distributions were largely consistent with the elevations of seed collection for the glasshouse experiment, except for *F. brayleyana*, which was collected at ~ 990 m, in the upper part of its range (Supplementary Table 1). Thus, the locations of seed collection also contributed to our consideration of habitat preferences for *F. ifflana* and *F. bourjotiana* to be lowland, and for *F. brayleyana* and *F. oppositifolia* to be upland.

Soil C:N ratio increased with elevation ($R^2 = 0.41$, $P < 0.01$) (Figure 1C) and soil $\delta^{15}\text{N}$ decreased with elevation ($R^2 = 0.57$, $P < 0.001$) (Supplementary Figure 3), suggesting that nitrogen availability declines with increasing elevation. The difference in soil $\delta^{15}\text{N}$ from the lowest site (40 m) to the highest site (1,550 m) was $\sim 5.7\text{‰}$ with a slope of -3.5‰ km^{-1} of elevation gain (Supplementary Figure 3). Soil $\delta^{13}\text{C}$ did not change significantly with elevation (Supplementary Figure 3).

3.2. Field observations: Stem diameter growth rates, LMA, foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Across an elevation gradient of 1,600 m in the Australian Wet Tropics, *Flindersia* species demonstrated a significant decline in stem diameter growth rates ($R^2 = 0.18$, $P < 0.01$). These declined by $ca 0.3 \text{ cm year}^{-1} \text{ km}^{-1}$ of elevation gain (Figure 2A).

The decline in GR among *Flindersia* species with elevation was accompanied by increasing LMA with increasing elevation ($R^2 = 0.22$, $P < 0.05$) (Figure 2B). The LMA increased by $ca 25 \text{ g m}^{-2} \text{ km}^{-1}$ of elevation gain. When averaged for each species within a site, the highest LMA was recorded for *F. oppositifolia* ($187 \pm 27 \text{ g m}^{-2}$) at Mount Bellenden Ker (1,550 m elevation) and the lowest for *F. ifflana* ($156 \pm 1 \text{ g m}^{-2}$) at Kuranda National Park (~ 300 m elevation). When averaged for each site, the highest LMA was recorded at Mount Bellenden Ker, and the lowest LMA ($\sim 142 \pm 3 \text{ g m}^{-2}$) was recorded at Kaaru Creek (~ 500 m elevation).

Foliar $\delta^{13}\text{C}$ also increased significantly with elevation by $ca 2.6\text{‰ km}^{-1}$ ($R^2 = 0.50$, $P < 0.01$) (Figure 2C). The average foliar $\delta^{13}\text{C}$ across the entire dataset was $-29.0 \pm 1.5\text{‰}$ ($n = 30$). The least negative $\delta^{13}\text{C}$ was observed for the mountaintop species, *F. oppositifolia* (-27.5‰ at 1,550 m) and most negative for *F. brayleyana* (-31.25‰ at 720 m).

Foliar $\delta^{15}\text{N}$ significantly declined with increasing elevation ($R^2 = 0.78$, $P < 0.001$) by $ca 8.5\text{‰ km}^{-1}$ of elevation gain (Figure 2D). Average foliar $\delta^{15}\text{N}$ across the entire dataset was $-0.05 \pm 3.9\text{‰}$ ($n = 30$). There was a large reduction of nearly 10‰ observed from the lowland site (4.8‰ at ~ 300 m elevation) to the mountaintop site (-5.2‰ at 1,550 m elevation).

3.3. Glasshouse experiment: Relative growth rate, root-to-shoot ratio, and LMA

Soil nutrient status had a significant effect on RGR, such that RGR was higher for plants in nutrient-rich compared to nutrient-poor

soil (Figure 3 and Table 2). The two species that responded most strongly to an increase in nutrient availability in terms of RGR were *F. ifflana*, the most lowland of the species, and *F. oppositifolia*, the mountaintop restricted species (Figure 3). There was also an interaction effect between Species and the extent of increase in RGR with increasing temperature. The lowland species showed steeper increases in RGR with increasing temperature than the upland species (Figure 3). This was confirmed by the *post hoc*, linear contrast where the slope of temperature response was larger in the lowland than in the upland species [$t_{(59)} = 3.8$, $p < 0.001$]. In general, the lowland species displayed an increasing RGR across the full temperature range, whereas the upland species did not.

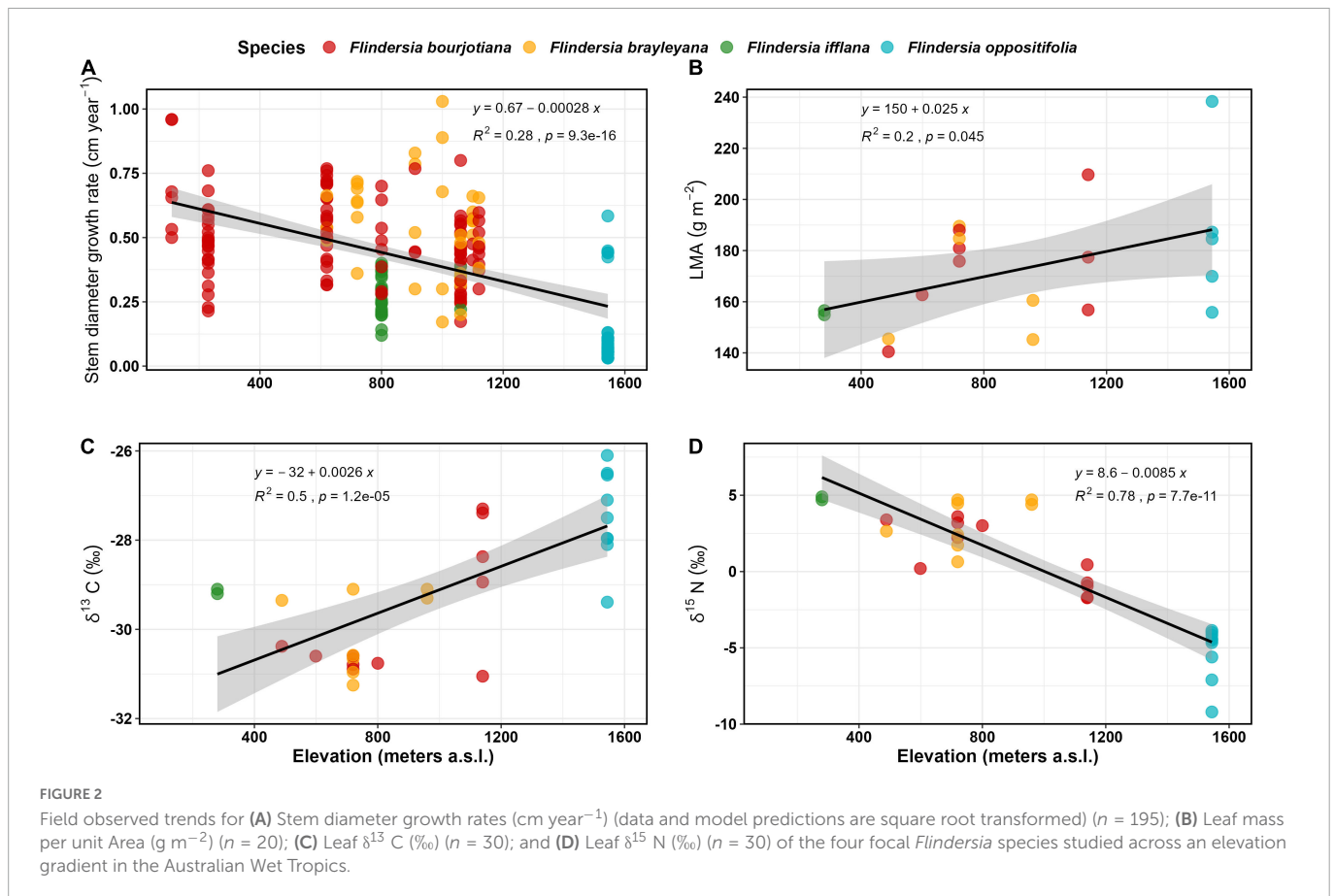
Root-to-shoot ratios (R:S) showed significant effects among Species and with Soil nutrient status (Table 2). The R:S was higher in nutrient-poor than in nutrient-rich soil, and there was a significant Species by Soil interaction (Table 2). This species-soil interaction was driven by the differential species response in the nutrient-poor Soil treatment. A pairwise, *post hoc* comparison among Species in the nutrient-poor Soil treatment, confirmed that the mountaintop-restricted species, *F. oppositifolia*, had a significantly higher R:S ratio compared to all other species [*F. ifflana*, $t_{(59)} = -3.6$, $p < 0.001$; *F. bourjotiana*, $t_{(59)} = -4.85$, $p < 0.001$; and *F. brayleyana*, $t_{(59)} = -4.18$, $p < 0.001$]. A pairwise, *post hoc* comparison among Species in the nutrient-rich Soil treatment indicated no significant differences among species. The highest R:S ratio for any Species by treatment combination occurred for *F. oppositifolia* in nutrient-poor Soil in the cold Temperature treatment (Figure 3).

There were no significant effects of Temperature, Soil nutrient status or Species on LMA in the glasshouse (Table 2 and Figure 3).

3.4. Glasshouse experiment: Foliar stable isotope composition

For foliar $\delta^{13}\text{C}$ in the glasshouse, there were significant main effects of Temperature, Soil nutrient status, and Species (Figure 4 and Table 2). Foliar $\delta^{13}\text{C}$ generally increased (became less negative) in plants grown in nutrient-rich Soil and increased with increasing Temperature. Average foliar $\delta^{13}\text{C}$ across the glasshouse dataset was $-29.7 \pm 1.4\text{‰}$. There was an increase in $\delta^{13}\text{C}$ of 1.3‰ associated with nutrient-rich compared to nutrient-poor Soil, and the rate of increase in $\delta^{13}\text{C}$ was $0.1\text{‰ per}^{\circ}\text{C}$ (Supplementary Table 4). A pairwise, *post hoc* comparison among Species showed that *F. brayleyana* had a more negative $\delta^{13}\text{C}$ than all other species [*F. ifflana*, $t_{(65)} = 3.68$, $p < 0.01$; *F. bourjotiana*, $t_{(65)} = 3.02$, $p < 0.05$; and *F. oppositifolia*, $t_{(65)} = -3.46$, $p < 0.01$]. Consistent with this, *F. brayleyana* in the field had also shown the most negative $\delta^{13}\text{C}$ among the four species (Figure 2).

Foliar $\delta^{15}\text{N}$ displayed a consistent variation with Soil nutrient status, which was the most important predictor in the model (Table 2). Plants in nutrient-rich Soil in the glasshouse displayed a higher $\delta^{15}\text{N}$ than those in nutrient-poor Soil; the increase in foliar $\delta^{15}\text{N}$ associated with nutrient-rich compared to nutrient-poor Soil according to the model was 2.0‰ (Supplementary Table 4). There was also a significant interaction between Species and Temperature (Table 2 and Figure 4). The *post hoc*, linear contrast between upland and lowland species showed that foliar $\delta^{15}\text{N}$ increased with temperature at a steeper rate in the upland species, *F. brayleyana* and *F. oppositifolia*, compared to the lowland species, *F. ifflana* and



F. bourjotiana [$t_{(62)} = -2.87, p < 0.01$]. The difference in slope between upland and lowland species was $0.13\text{‰ per }^{\circ}\text{C}$.

4. Discussion

We investigated trends in tree growth and leaf functional traits along an elevation gradient in the Australian Wet Tropics using a single, regionally important genus to gain insight into the responses of closely related species with differing elevational distributions. Observations in tropical rainforests on other continents have shown that tree growth rates and foliar $\delta^{15}\text{N}$ typically decline with elevation (Bauters et al., 2017; Malhi et al., 2017), whereas LMA and foliar $\delta^{13}\text{C}$ typically increase with elevation (Vitousek et al., 1990; Mumbanza et al., 2021). We confirmed from our field-based observations that similar trends also occur in *Flindersia* species in Australian tropical rainforests. These trends with elevation could be a result from at least three important drivers: decreasing temperatures, decreasing soil nutrient availability, and changes in species composition (Malhi et al., 2010; Rapp, 2010). Using a factorial glasshouse experiment, we attempted to disentangle these potential drivers to better understand their relative roles in controlling plant form and function. We detected direct effects of temperature and nutrient availability on some of the examined traits, and our results also suggested that some variation could be attributed to species adaptations to their preferred elevational ranges. Our experiment provided new insights in instances where the observed field trends could not be reproduced in the glasshouse by varying temperature and soil nutrient availability in isolation.

4.1. Growth rates, biomass allocation strategies and LMA

The observed decline in stem diameter growth rates among *Flindersia* species with increasing elevation was accompanied by a decline in MAT, i.e., $\sim -5.3^{\circ}\text{C km}^{-1}$ (Figure 1A), along with increasing C:N ratio in soils, indicative of declining nitrogen availability (Figure 1C). Previous studies have reported similar declines in growth rates with MAT among closely related *Weinmannia* species, in the Peruvian Andes (Rapp, 2010) and the southwest Andes (Tito et al., 2018). The effect of declining temperature with elevation drives slower metabolic rates, while slower nitrogen mineralization rates likely further contribute toward growth reductions (He et al., 2016; Gong et al., 2020). Our glasshouse experimental results also supported the idea that slower growth rates with increasing elevation could be partly explained by changes in species composition. Although species' mean RGR across the experimental treatments did not reflect the species' site of origin on the elevation gradient (i.e., RGR increasing with decreasing elevation of origin), we did find that the RGR of the upland species did not respond as strongly to temperature as in the lowland species. Interestingly, the mountaintop species, *F. oppositifolia*, displayed similar growth rates compared to the lowland collected species under lowland temperatures and in nutrient-rich soil (Figure 3). This bodes well for this mountaintop-restricted species, at least from an *ex situ* conservation perspective, in terms of its potential for growth in plantings at lower elevations (Primack et al., 2021). It may also indicate that warming temperatures *per se*, which are predicted to eliminate its current climate niche (Costion et al., 2015), may

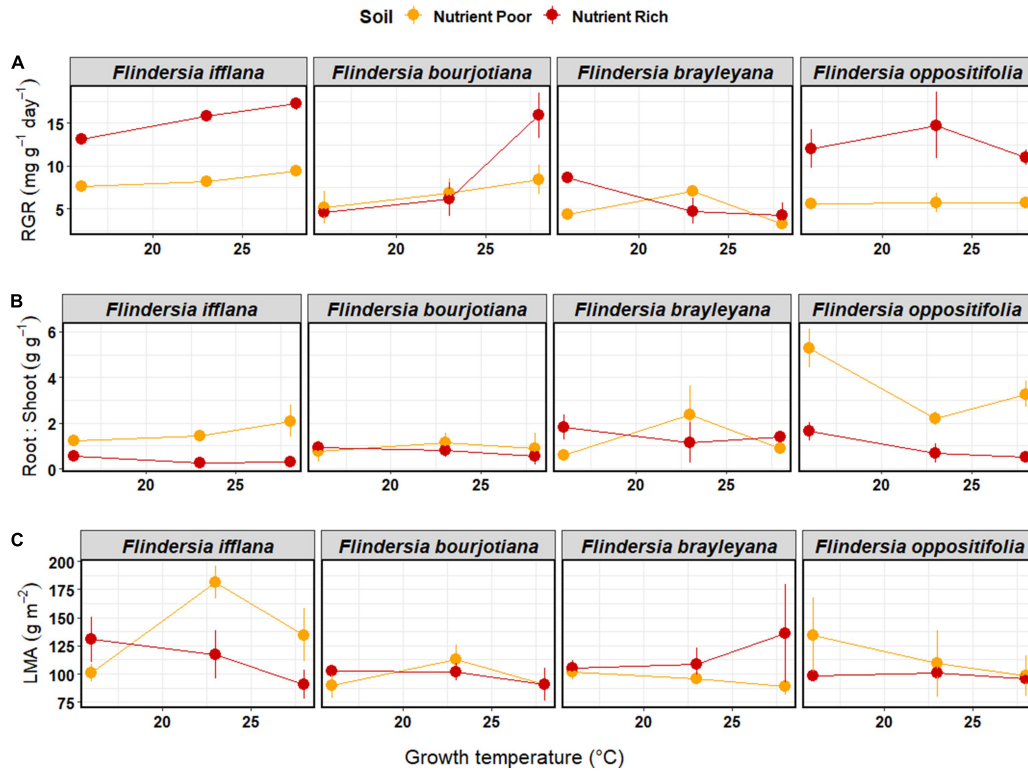


FIGURE 3

Means ($\pm 1SE$) of (A) relative growth rate ($\text{mg g}^{-1} \text{day}^{-1}$), (B) root-to-shoot ratio (g g^{-1}), and (C) leaf mass per unit area (g m^{-2}) among temperature and soil nutrient treatments (nutrient-rich soil = red, nutrient-poor soil = orange) in the glasshouse experiment. Each dot represents a mean of three individual saplings. Species are arranged left to right according to their observed elevation ranges, with leftmost being lowland and rightmost being mountaintop.

not negatively impact growth *in situ*, with optimal growth of this species occurring at temperatures higher than currently experienced. However, other factors associated with warming, such as increasing atmospheric water stress (Bauman et al., 2022b), and effects on seed bank dynamics (Liyanage et al., 2022), along with biotic interactions, may negatively impact survival of such mountaintop endemic plants (Cheesman and Winter, 2013).

In our glasshouse experiment, we observed that Soil nutrient status and Species had significant impacts on R:S ratios, but that the chamber temperature did not. This was exemplified by the observation that the mountaintop species in our experiment had a very high R:S under nutrient-poor, cold conditions, as has been reported with other montane taxa in their native growth provenance across the tropics (Wu et al., 2013; Fahey et al., 2016). Biomass allocation strategies under resource poor conditions have been explained by the optimal partitioning theory, which predicts that plants generally increase allocation of biomass toward the organs that acquire the most limiting resources (Kobe et al., 2010; Poorter et al., 2012), the roots in this case. Plants generally prefer a more conservative approach by investing more in roots under cold temperatures and lower nutrient availability and more in above ground parts with warmer temperatures and higher nutrient availability (Girardin et al., 2014). In general, Australian rainforest plants have adapted to nutrient-poor soils (Congdon and Herbohn, 2009; Gleason et al., 2010). However, the relatively higher allocation of biomass to roots in mountaintop plants may also indicate an adaptive functional strategy toward shallow soils and toward physical support from strong winds, in addition to

nutrient foraging (Körner, 2007; Girardin et al., 2010; Wu et al., 2013). These observations suggest that an important trait that allows *F. oppositifolia* to compete successfully in the mountaintop environment is a greater capacity to allocate biomass to roots in cold, nutrient-poor conditions, which was not observed in the lowland species in the glasshouse under similar growth conditions.

Our observation of an increase in LMA with elevation compares well with field-based studies in the tropics (Neyret et al., 2016; Martin et al., 2020). The importance of LMA as an indicator of plant growth strategies is well established in the literature (Westoby et al., 2002; Poorter et al., 2009). LMA is the product of leaf thickness and density (Roderick et al., 1999), and studies have reported that plants generally display thicker and/or denser leaves in more stressful environments (Poorter et al., 2009). Higher LMA generally corresponds to the slow end in the fast-slow continuum of the leaf economic spectrum, indicative of a more conservative rather than acquisitive strategy (Wright et al., 2004). It has been suggested that higher LMA at lower temperatures might come about because of reduced leaf expansion rates (Westoby et al., 2002; Poorter et al., 2009; Van De Weg et al., 2012). Other factors potentially contributing to observed variation in LMA across elevation could be differences in incident light across sites given differences in cloud cover (Martin et al., 2020). Although, we did not quantify variation in irradiance where leaves were collected along the elevation gradient, all leaves in the study were 'fully exposed' sunlit leaves, but we must acknowledge this could have been an additional factor contributing to the observed variability in LMA.

TABLE 2 Summary table of the type III ANOVA results from linear regressions for each of the response variables against growth temperature, soil nutrient status, species and interactions with species from the glasshouse experiment.

Predictors	log (RGR)			R:S			1/sqrt (LMA)			$\delta^{13}\text{C}$			$\delta^{15}\text{N}$							
	Sum of squares	F statistic	DF	p	Sum of squares	F statistic	DF	p	Sum of squares	F statistic	DF	p	Sum of squares	F statistic	DF	p				
(Intercept)	2.23	17.69	1	<0.001	0.87	1.02	1	0.319	0.153	1,045.0	1	<0.001	2,782.8	1,950.4	1	<0.001	4.48	5.30	1	0.025
Temperature	0.17	1.38	1	0.244	0.02	0.28	1	0.595	-	-	-	-	15.23	10.67	1	0.002	1.04	1.23	1	0.271
Species	1.88	4.96	3	0.004	18.45	7.088	3	<0.001	0.001	2.10	3	0.108	25.30	5.92	3	0.001	5.49	2.16	3	0.10
Soil	1.61	12.74	1	0.001	6.72	7.75	1	0.007	-	-	-	-	14.16	9.93	1	0.002	73.55	87.02	1	<0.001
Temperature \times Species	2.64	6.95	3	<0.001	7.19	2.67	3	0.050	-	-	-	-	-	-	-	-	10.50	4.14	3	0.010
Soil \times Species	1.38	3.65	3	0.017	21.22	8.15	3	<0.001	-	-	-	-	-	-	-	-	-	-	-	-
Residuals	7.42	NA	59	NA	51.19	NA	59	NA	51.19	NA	67	NA	92.73	NA	65	NA	52.40	NA	62	NA

The *p*-values in bold indicate significant effects. Where interaction effects or a predictor itself were not significant and their removal resulted in a lower AIC, a simpler model has been shown. The removal of an interaction or a predictor has been indicated with '-'.[†]

We expected LMA, being a key growth trait reflecting acclimation to stress and/or resource poor conditions (Poorter et al., 2009), should have responded in our experimental treatments to temperature and/or soil nutrient availability. Surprisingly, we did not observe changes in LMA in our glasshouse experiment as we would have expected based on the observed field trend. This could possibly be explained by ontogenetic differences, insofar as mature trees were sampled in the field compared to saplings in the glasshouse experiment. Ontogeny has been previously highlighted as important in comparing trait measurements between experimental and field studies, especially for tropical plants (Poorter et al., 2012; Scalón et al., 2022).

4.2. Foliar $\delta^{13}\text{C}$ and elevation

The influence of climate and soil properties in the field was reflected in the foliar isotopic composition with increasing elevation. Foliar isotope ratios are useful proxies to understand plant photosynthetic water use and nutrient dynamics in tropical ecosystems (Cernusak et al., 2007a; Craine et al., 2015). We observed an overall trend of increasing foliar $\delta^{13}\text{C}$ (Figure 2C) with increasing elevation (ca $\sim 2.6\text{‰ km}^{-1}$) among the *Flindersia* trees that we sampled in the Australian Wet Tropics. This can be compared to global studies on C_3 plants in humid forests, where on average $\sim 1.3\text{‰ km}^{-1}$ increase in foliar $\delta^{13}\text{C}$ has been reported with elevation (Li et al., 2009). Likewise, a study reported a change from -29.5‰ in lower elevation sites to as high as -24.8‰ in montane sites of Hawaii for a single species, *Metrosideros polymorpha* Gaudich (Cordell et al., 1998). Such large intraspecific variation has been attributed to increase in species' water-use efficiency with increasing elevation and its inherent adaptive plasticity to variable environmental conditions (Cordell et al., 1998; Peri et al., 2012). Studies have also reported variation in foliar $\delta^{13}\text{C}$ with other environmental attributes such as precipitation, soil nutrients, solar radiation, and VPD (Vitousek et al., 1990; Chen et al., 2017; Zou et al., 2019; Bauman et al., 2022a). Variation in foliar $\delta^{13}\text{C}$ with elevation can also result from the influence of leaf morphology (leaf thickness or LMA, for example), which leads to longer diffusion pathways for CO_2 into the leaf and decreases the internal-to-ambient CO_2 concentration ratio (c_i/c_a) and hence causes enrichment of foliar $\delta^{13}\text{C}$ in montane flora (Körner et al., 1986; Prentice et al., 2014). Another contributing factor could be increased viscosity of water with lower temperature, which causes larger frictional resistance to water transport and hence a partial closure of stomata thereby decreasing c_i/c_a and increasing foliar $\delta^{13}\text{C}$ (Prentice et al., 2014).

Two aspects of our observations of foliar $\delta^{13}\text{C}$ in the glasshouse went in opposite directions to the trends in the field. We did observe changes in foliar $\delta^{13}\text{C}$ in response to temperature, but the direction of this response was opposite to that in the field. Foliar $\delta^{13}\text{C}$ became less negative with increasing experimental temperature, whereas in the field it was more negative at lower (warmer) than at higher (cooler) elevations. Such a trend, as observed in the glasshouse, of increasing $\delta^{13}\text{C}$ with increasing temperature has been previously reported from arid or semi-arid sites (Chen et al., 2017), and could be explained by increased VPD at warmer temperatures, which causes stomatal closure (Grossiord et al., 2020). Such conditions lead to a lower c_i/c_a resulting in a higher $\delta^{13}\text{C}$ with increasing VPD (Cernusak et al., 2013). In our glasshouse study, VPD increased with increasing temperature, and so when plotted against VPD, foliar $\delta^{13}\text{C}$

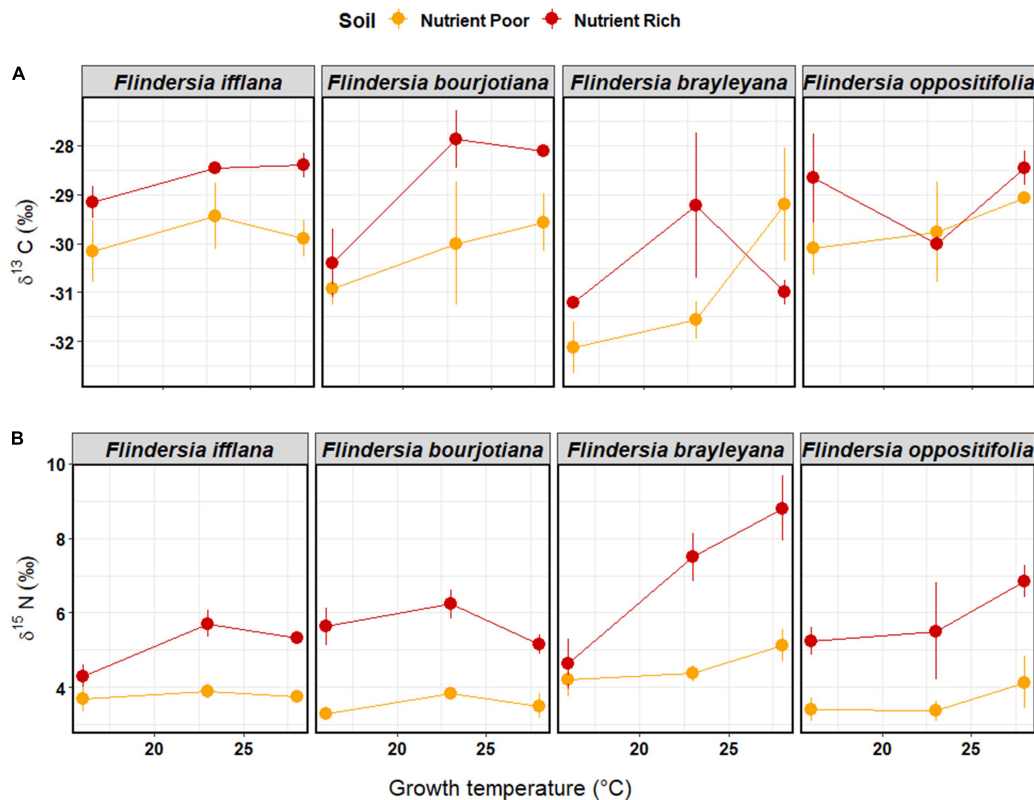


FIGURE 4

Means ($\pm 1SE$) of (A) leaf $\delta^{13}C$ (‰) and (B) leaf $\delta^{15}N$ (‰) among temperature and soil nutrient treatments (nutrient-rich soil = red, nutrient-poor soil = orange) in the glasshouse experiment. Each dot represents a mean of three individual saplings. Species are arranged left to right according to their observed elevation ranges, with leftmost being lowland and rightmost being mountaintop.

increased with increasing VPD (Supplementary Figure 6), as would be expected, all else being equal. Interestingly, for the field collections in the Australian Wet Tropics, the annual mean VPD also decreases with decreasing temperature as elevation increases (Bauman et al., 2022b; Supplementary Figure 2). This suggests that the role of VPD in driving field trends in foliar $\delta^{13}C$ is insufficient to overcome drivers pushing in the other direction as elevation increases to enrich foliar $\delta^{13}C$.

The second aspect of our glasshouse results for foliar $\delta^{13}C$ that did not agree with the field trends was the response to nutrient availability. Plants grown in nutrient-rich soil had higher $\delta^{13}C$ than those grown in nutrient-poor soil (Figure 4). This was expected, based on previous studies (Cernusak et al., 2007b; Palma et al., 2020), and the known physiological response of lower c_i/c_a in leaves with a higher photosynthetic capacity resulting from higher nitrogen concentrations (Cernusak et al., 2013). However, in the field, we demonstrated that nutrient availability likely decreases with increasing elevation, as indicated by the increase in soil C:N ratio (Figure 1C). Thus, if we consider this in isolation, it indicates an opposite response to that observed in the glasshouse: foliar $\delta^{13}C$ in the field became higher with increasing elevation as soil nitrogen availability likely decreased, rather than increased.

We suggest that there are two driving factors in the field that can explain foliar $\delta^{13}C$ responses to elevation, and which are apparently sufficient to overcome effects of temperature on VPD and nutrient availability that push in the opposite direction. The first is changes in leaf structure that occurred in the field with

increasing elevation, but which were absent in the glasshouse. The increase in LMA with increasing elevation in the field would likely be indicative of a greater tortuosity for diffusion of CO_2 inside the leaf, increasing the intercellular air space diffusion resistance, and thicker cell walls, increasing the mesophyll diffusion resistance, both ultimately lowering chloroplastic CO_2 concentrations and therefore discrimination against ^{13}C . The effect of more robust leaf structure was identified by Vitousek et al. (1990) as the most potent driver of foliar $\delta^{13}C$ trends with elevation in *Metrosideros polymorpha* Gaudich. in Hawaii. The second driving factor in the field that did not occur in the glasshouse is the decrease in atmospheric pressure that accompanies an increase in elevation. Effects of this on ^{13}C discrimination are less mechanistically understood, but it is known that a decrease in oxygen partial pressure in the chloroplast can increase the efficiency of carboxylation (Farquhar and Wong, 1984), which may further decrease discrimination against ^{13}C . Thus, our glasshouse results suggest that the drawdown of chloroplastic CO_2 in the field is likely to be related to the low atmospheric pressure at higher elevations and changes in leaf structure that increase the diffusion resistance through the internal airspace and mesophyll (Vitousek et al., 1990; Wang et al., 2017), neither of which occurred in the glasshouse with a change in temperature. Our glasshouse results also show that a change in water viscosity that occurs with temperature was not a strong enough driver of variation in foliar $\delta^{13}C$ to overcome the effect of the increases in VPD that coincided with increasing temperature (Supplementary Figure 6).

Given the known relationship between mean annual precipitation (MAP) and foliar $\delta^{13}\text{C}$ (Cernusak et al., 2013; Cornwell et al., 2018), it is reasonable to ask whether a difference in soil water availability between the field and the glasshouse might have impacted our results. In the glasshouse, the experimental pots were watered to field capacity by hand each day, and we therefore feel confident that they did not experience substantive soil water deficits. With respect to the field collections, the Australian Wet Tropics in general is characterized by MAP approaching and exceeding 2,000 mm (Turton et al., 1999), a range in which foliar $\delta^{13}\text{C}$ in tropical rainforests is largely insensitive to MAP (Leffler and Enquist, 2002; Diefendorf et al., 2010). In a recent analysis, it was shown that mean climatological water deficit was not a significant predictor of tree growth rates across forests in the Australian Wet Tropics similar to those that we sampled (Bauman et al., 2022a). Furthermore, sap flow measurements at lowland, mid-elevation, and high elevation sites in the Australian Wet Tropics indicated that transpiration at the tree level is largely unresponsive to seasonal variations in soil moisture (McJannet et al., 2007; Binks et al., 2022). At the Daintree Rainforest Observatory, a lowland site, a multi-year throughfall exclusion experiment resulted in no response of foliar $\delta^{13}\text{C}$ in the treated plot compared to the control plot (Pivovarov et al., 2021). Finally, mean foliar $\delta^{13}\text{C}$ values in our study for the three species with broader elevation ranges were very similar in the glasshouse compared to the field (*F. ifflana*, -29.3‰ vs. -29.2‰ ; *F. bourjotiana*, -29.6‰ vs. -29.6‰ ; *F. brayleyana*, -30.7‰ vs. -30.5‰), as can also be seen in Figures 2, 4. The mountaintop species, *F. oppositifolia*, had a mean value in the glasshouse of -29.3‰ compared to -27.5‰ in the field. This enrichment of approximately 2‰ for *F. oppositifolia* grown in the field at 1,550 m elevation compared to the plants grown near sea level in the glasshouse cannot have resulted from a limitation of soil water availability on the mountaintop; observed MAP on the top of Mount Bellenden Ker near where the trees were sampled exceeds 7,000 mm (McJannet et al., 2007). The WorldClim gridded climate product provided an estimate of 5,650 mm (Supplementary Table 1), but this reflects a known bias in coarser scale products for this site due to the complex topography (Turton et al., 1999). These considerations combined argue strongly against soil water deficit as an important driver of the foliar $\delta^{13}\text{C}$ data that we present in this paper.

4.3. Foliar $\delta^{15}\text{N}$ and elevation

For foliar $\delta^{15}\text{N}$ we found a marked decrease with increasing elevation ($\sim -8.5\text{‰ km}^{-1}$ elevation), which is a much larger change compared to most studies in the tropics (Liu et al., 2007; Liu and Wang, 2010; Bauters et al., 2017; Wang et al., 2019). For instance, a study from Mt Gongga, in the southwest region of China, reported on average $\sim -1.3\text{‰}$ difference from 1,100 to 4,900 m elevation (Li et al., 2009); and -1.4‰ to 14.2‰ across an elevation gradient from 900 to $\sim 4,000$ m in the Ethiopian Rift valley (Liu et al., 2007). The closest to our observation comes from one study involving *Pinus spp.* in Nepal that reported nearly -8‰ difference over 800 m elevation (Sah and Brumme, 2003). These trends are known to be related in part to a decline in $\delta^{15}\text{N}$ of soil nitrogen with elevation (Wang et al., 2019). We did find some evidence of such a relationship between foliar $\delta^{15}\text{N}$ and that of the soil nitrogen in our study (Supplementary Figure 5). The enrichment of $\delta^{15}\text{N}$ at warmer, lowland sites is thought to result from a more open nitrogen cycle, where nitrogen loss pathways discriminate against the heavier isotope, ^{15}N , leaving the residual

nitrogen pool ^{15}N enriched (Martinelli et al., 1999; Ma et al., 2012; Peri et al., 2012; Wang et al., 2019). The marked decline in foliar $\delta^{15}\text{N}$ that we observed in the Australian Wet Tropics suggests that a slowing and tightening of the nitrogen cycle with increasing elevation is likely a key driver of decreasing tree growth rates.

Furthermore, under glasshouse conditions we did observe differences in foliar $\delta^{15}\text{N}$ consistent with field-based trends, although the observed variation was generally not as large as seen in field. The differences in foliar $\delta^{15}\text{N}$ in the field versus the glasshouse might be related to soil development processes. For example, the trends in the glasshouse reflect a snapshot of the species' growth within the experimental period reflecting foliar signatures based on available soil N. On the other hand, those observed in the field partly reflect the ecosystem nitrogen pool that would have developed from nutrient cycling processes integrated over millennia (Craine et al., 2015). In our glasshouse study, variation in foliar $\delta^{15}\text{N}$ induced by soil nutrient status was still pronounced, with higher foliar $\delta^{15}\text{N}$ in nutrient-rich ($\sim 5.9\text{‰}$) compared to nutrient-poor ($\sim 3.8\text{‰}$) soils, averaged for all species. We suggest that this increase in foliar $\delta^{15}\text{N}$ in the nutrient-rich pots can be explained by greater opportunity for N loss from the pots by $\delta^{15}\text{N}$ fractionating pathways than in the case where nutrient availability is low and available N is effectively captured by the soil-plant system. In support of this, we also observed that foliar $\delta^{15}\text{N}$ varied as a function of root mass (Supplementary Figure 7), indicating the influence of larger root systems in capturing available nitrogen, thereby limiting loss pathways from the soil-plant system that would otherwise leave the residual $\delta^{15}\text{N}$ in the system ^{15}N enriched (Baumgartner et al., 2021).

We observed a significant interaction between Species and Temperature for foliar $\delta^{15}\text{N}$ in the glasshouse study (Table 2). This indicated that as growth temperature increased, foliar $\delta^{15}\text{N}$ tended to increase in the upland species, but not in the lowland species (Figure 4). We suggest that the species difference in foliar $\delta^{15}\text{N}$ indicates a better ability of the lowland species to absorb increasingly available nitrogen as increasing temperatures drove faster nitrogen mineralization rates in the experimental pots. The lowland species, in turn, were able to take advantage of this by increasing their relative growth rates under these conditions (as see in Figure 3). The upland species, on the other hand, have likely evolved to function in conditions of relatively low nitrogen availability, and lacked the capacity to ramp up their nitrogen uptake to the same extent in response to the warmer growth temperatures. This would have allowed greater nitrogen losses from the soil-plant systems, which then caused increases in foliar $\delta^{15}\text{N}$. Thus, our results indicate that there are likely important belowground traits related to nutrient absorption capacity that distinguish *Flindersia* species with differing habitat preferences along the elevation gradient. It is also important to note the role of soil microbes in controlling the $\delta^{15}\text{N}$ of the soil-plant system, and in modulating soil nitrogen transformations that can lead to nitrogen isotope fractionations (Houlton et al., 2006; Pajares and Bohannan, 2016; Hestrin et al., 2019); although we recognize the importance of these processes, we did not quantify them in the present study.

4.4. Concluding remarks

Climate change is driving warmer temperatures in the tropics, and it has been suggested that these could potentially have negative

effects on tropical tree growth, with implications for biomass productivity and ecosystem functioning (Hatfield and Prueger, 2015; Malhi et al., 2015). It is important to recognize that responses of tropical trees to global warming involve a myriad of interacting factors. Our study demonstrated that altering temperature in isolation of other factors that covary in nature can lead to counterintuitive results, for example in the case of foliar $\delta^{13}\text{C}$. In natural ecosystems, temperature itself may only indirectly drive impacts of warming. For example, mortality in mature rainforest trees of the Australian Wet Tropics has been increasing in recent decades, but the trend in increase in tree mortality can be better attributed to increasing air VPD, which has accompanied the increase in air temperature (Bauman et al., 2022b). We also observed in this study that elevation patterns in tree function are linked to changes in nutrient availability, and even to the change in atmospheric pressure that coincides with a change in elevation.

Adaptations of *Flindersia* species to their different preferred habitats along the elevation gradient were evident in their responses to temperature in the glasshouse. We found that upland species did not show increasing growth rates with increasing temperatures, whereas lowland species did, indicating their ability to acclimate to warmer conditions. In addition, we observed that a distinguishing feature of a mountaintop-restricted species was a proportionally larger allocation toward roots under nutrient-poor, cold conditions. This feature is known to help plants with physical support from higher wind speeds on tropical mountaintops, and likely contributes to nutrient foraging when soil nutrients are scarce (Körner, 2003). As the climate warms, impacts on nutrient cycling at the ecosystem scale may lag direct effects of temperature on tree metabolism; understanding how such changes will interact with species traits is a formidable, but an important, challenge.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

ASR and LAC conceived the manuscript with inputs from AWC and HF-M. ASR conducted field data collection and designed the experiment under the supervision of LAC and AWC. DMC helped develop species selection. NDP facilitated seed collection. ASR conducted the data analysis with inputs from HF-M and LAC. ASR wrote the first draft with LAC. All authors edited and approved the final draft for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2023.1089167/full#supplementary-material>

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