

# Strong site and provenance effects on tropical tree growth and survival, but mixed evidence for local adaptation

Kali Middleby<sup>1</sup>, Lucas A. Cernusak<sup>1</sup>, Martin F. Breed<sup>1</sup>, Darren M. Crayn<sup>1</sup>, Susan G.W. Laurance<sup>1</sup>, Noel Preece<sup>1</sup>, Penny van Oosterzee<sup>1</sup>, Jayden Engert<sup>1</sup>, and Alexander W. Cheesman<sup>1</sup>

<sup>1</sup>Affiliation not available

November 26, 2024

Kali B. Middleby<sup>1</sup>, Lucas A. Cernusak<sup>1</sup>, Martin F. Breed<sup>2</sup>, Darren M. Crayn<sup>3,4</sup>, Susan G.W. Laurance<sup>1</sup>, Noel Preece<sup>1,5,6</sup>, Penny van Oosterzee<sup>1,5,6</sup>, Jayden Engert<sup>1</sup>, and Alexander W. Cheesman<sup>1</sup>

<sup>1</sup> Centre for Tropical Environmental Sustainability Science, James Cook University Nguma-Bada Campus, McGregor Road, Smithfield, QLD, Australia

<sup>2</sup> College of Science and Engineering, Flinders University, Bedford Park, SA, Australia

<sup>3</sup> Australian Tropical Herbarium, James Cook University Nguma-Bada Campus, McGregor Road, Smithfield, QLD, Australia

<sup>4</sup> ARC Centre of Excellence for Indigenous and Environmental Histories and Futures, James Cook University Nguma-Bada Campus, McGregor Road, Smithfield, QLD, Australia

<sup>5</sup> Biome 5 Pty Ltd., Atherton, QLD, Australia

<sup>6</sup>Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia

## ABSTRACT

Restoring tropical rainforests is vital for mitigating climate change and conserving biodiversity. Appropriate seed-sourcing strategies are important for ensuring the success of restoration efforts, but require species-specific and context-dependent information, such as the strength of local adaptation. With studies of local adaptation severely lacking for tropical rainforest tree species, the current industry default is to source seed locally, which may not be beneficial in a rapidly changing climate. We therefore sought to identify the effects of provenance, site, and their interaction on the growth and survival of 16 tropical tree species commonly used for rainforest restoration in the Australian Wet Tropics. Saplings from lowland and upland populations were planted in common gardens across three field sites with contrasting climatic and edaphic conditions. We observed consistent site effects on growth, with all species performing better at the lowland, high-nutrient site compared to the lowland, low-nutrient and upland sites. Provenance effects were observed for both growth and survival, but evidence for local adaptation was mixed, with the lowland provenance often outperforming the upland provenance across most sites. Interestingly, species-variation in the effects of provenance was related to species wood density, with provenance effects more pronounced in faster-growing species. Together, these findings highlight the complexity of local adaptation in tropical tree species, which brings a note of caution to the current practice of sourcing seed locally.

## KEYWORDS

Provenance, reciprocal transplant, climate change, restoration, ecotypes

## INTRODUCTION

Tropical rainforests represent a disproportionate and dynamic component of the world’s carbon budget (Mitchard 2018, Friedlingstein *et al.* 2022), contain a majority of Earth’s terrestrial biodiversity (Barlow *et al.* 2007, Gibson *et al.* 2011), and provide a diverse array of ecosystem services (Watson *et al.* 2018). Despite their significance, these ecosystems are under severe anthropogenic pressure, with an estimated 17% reduction in moist tropical forest extent from 1990 to 2019 (Vancutsem *et al.* 2021). At the same time, active restoration of terrestrial ecosystems is essential for addressing global challenges such as climate change, biodiversity decline, and land degradation (Girardin *et al.* 2021). The latest IPCC report (Riahi *et al.* 2022), highlights afforestation, reforestation, and revegetation perhaps in addition to improved forest management, agroforestry, and soil carbon sequestration as the primary CO<sub>2</sub> removal methods currently in use. The United Nations (UN) declared 2021-2030 the Decade of Ecosystem Restoration (United Nations General Assembly 2019). However, the increasing frequency of hot, dry periods is exacerbating global tree mortality (Hammond *et al.* 2022) and is predicted to increase the frequency of lethal canopy temperatures being reached in tropical forests (Doughty *et al.* 2023), posing a significant threat to the success of restoration efforts.

In response to climate change, plants can migrate, adapt, or become extinct (Corlett & Westcott 2013, Merila & Hendry 2014). However, the rapid rate of anthropogenic climate change and the shallow latitudinal temperature gradient in the tropics mean that migration is largely restricted to upward shifts in elevation (Colwell & Feeley 2024). Additionally, the long generation times of forest tree species limit their ability to adapt quickly, making intraspecific phenotypic variation – both genetic variation accumulated over generations and phenotypic plasticity – crucial for adaptation (Merila & Hendry 2014). When variation exists for divergent selection to act on, local adaptation can result in local populations with a fitness advantage over nonlocal populations in their home site (Brancalion *et al.* 2018, Muehleisen *et al.* 2020). Understanding and leveraging intraspecific variation is therefore essential for assessing and enhancing the success of restoration plantings in the face of rapid climate change.

One strategy to ensure that restoration plantings are successful in establishing resilient forests is the appropriate choice of seed sources. Restoration guidelines provide advice on how to maintain the genetic diversity and adaptive capacity of restored forest populations through the consideration of the geographic origin of seed, i.e. provenance (Offord & Meagher 2009, McDonald *et al.* 2016, Malavasi *et al.* 2018). Although a strategy of selecting local provenances has traditionally been preferred by practitioners (Cooper *et al.* 2018), this can reduce fitness in cases when forest fragmentation results in inbreeding (Schlaepfer *et al.* 2018) or when rapid climate change causes a mismatch between the current or future climate with the historic conditions a population is adapted (Aitken & Whitlock 2013, Gellie *et al.* 2016). These issues have led to the recommendation of alternative provenancing strategies incorporating non-local seed sources (Breed *et al.* 2013, Jordan *et al.* 2024). Given the strong role climate can have in driving selection (Steane *et al.* 2014, Cordero *et al.* 2021, Ravnet *et al.* 2024), the matching of seed sources to future climates (known as predictive or climate-adjusted provenancing) aims to introduce to an area genetic material that is better adapted and therefore also more resilient to climate change (Breed *et al.* 2013).

Despite the known advantages that strategies such as climate-matching provenance can have for restoration outcomes, the current industry default in rainforest restoration plantings is to source seed locally (Cooper *et al.* 2018). A key challenge in adopting alternative provenance selection in tropical rainforests is the extensive genetic information required to recommend a suitable strategy. Evidence for local adaptation requires direct evidence of local populations having fitness advantages over non-local populations, with full life-cycle analysis under reciprocal common garden conditions being considered the gold standard for determining true local

adaptation (Kawecki & Ebert 2004, Meek *et al.* 2022, Schwinning *et al.* 2022). Synthesis studies to date are heavily biased toward temperate species of commercial importance with very few, if any, tropical trees included (Hereford 2009, Matesanz & Ramirez-Valiente 2019). Their findings also reveal how the presence and strength of local adaptation are species and context-dependent. This limits our understanding of the prevalence and strength of local adaptation in tropical rainforest trees, which typically have lower population densities than temperate species, but high reproductive efficiency over large distances maintaining similar levels of genetic diversity (Degen & Sebbenn 2015). However, provenance trials to test for local adaptation are highly resource-intensive (Sorket *al.* 2013) and typically focus on a single species. This has limited the broad applicability of climate-matching provenance strategies in tropical systems where forests are extremely speciose and understanding the genetic background of each species is not feasible.

While a ‘one-size fits all’ approach to provenancing is generally not recommended or ideal, the combination of extremely high species diversity in tropical rainforests, and the limited resources available for restoration activities necessitates a simplified, easy-to-implement provenancing strategy. One possibility could be grouping the strategy according to species plant functional traits, such as wood density, that describe the *slow-fast* life-history continuum (Reich 2014). Faster-growing species such as pioneers have shorter lifespans and earlier reproductive capacity than slower-growing species such as mature-phase species. As such, early successional stage species may show higher rates of molecular evolution and therefore be more likely to have developed local adaptation than slower-growing species (Smith & Donoghue 2008, Smith & Beaulieu 2009, Müller & Albach 2010). However, with studies of local adaptation severely lacking for tropical rainforest tree species, there is currently insufficient experimental evidence to support this. Additionally, while meta-analyses are useful to discern the patterns and drivers of local adaptation in studies across multiple species, these studies often vary in methodology, site maintenance, and conditions that are not easily accounted for. There is therefore a need for multi-species studies of local adaptation in tropical trees that are key to rainforest restoration.

We investigated the prevalence of local adaptation in tropical rainforest tree species commonly used in restoration plantings in the Australian Wet Tropics. To do so we established three field-based provenance trials, including an upland and lowland site that differ in climate but have similar high-nutrient soils, and an additional lowland site on a low-nutrient soil. Saplings of 16 species were sourced from lowland and upland populations and reciprocally planted at each site, where initial growth and survival were monitored over 1.5 years. Specifically, we tested the following questions:

1. How do provenance, site, and provenance  $\times$  site interactions affect sapling growth and survival?
2. If provenance  $\times$  site interactions exist, do local provenances outperform non-local provenances at their local site?
3. If there is variation across species in their provenance differentiation, is this more pronounced in faster-growing species?

## METHODS

### 2.1 Common Garden sites

This experiment, part of the ‘TropAdapt’ project (<https://tropadapt.org/>) was conducted across three common garden trials established within the Wet Tropics bioregion of far north Queensland, Australia: two in the coastal lowlands and one in the uplands. The first lowland site is located at the Daintree Rainforest Observatory (DRO) in Cape Tribulation (-16.10449 degS, 145.4511 degE) with an elevation of 52 m (a.s.l.), mean annual temperature (MAT) of 24.5 degC and a mean annual precipitation (MAP) of 3026 mm. The soil at the site is acidic, dystrophic, brown dermosol, formed in the colluvium from the metamorphic and granitic mountains to the west (Murtha 1989). The second lowland site was established on an old airstrip in Cow Bay (-16.22406 degS, 145.4220 degE) with a MAT of 24.4 degC and a MAP of 3439 mm. Although soils in the area

were originally dominated by haplic, dystrophic, red ferrosols formed on an alluvial fan derived from basalt (Murtha 1989), an anthropogenic reworking of the site and augmentation with sand and gravels to form the airstrip have left the soils poorly structured. The upland study site is in the southern Atherton Tablelands (-17.43025 degS, 145.5153 degE) on Thiaki Creek Nature Reserve (<https://www.biome5.com.au/thiaki>) at an elevation of 980 m a.s.l. It has a MAT of 19 degC and receives a MAP of 2264 mm. The site is on a formed from Cainozoic Basalt (Malcolm *et al.* 1999). The property was previously managed as a cattle pasture for approximately 70 years, and subsequently used as a research site for several previous reforestation experiments (Charles *et al.* 2018) (Preece *et al.* 2015, Preece *et al.* 2017). The common garden plot used for this study is dominated by exotic grass species (e.g. *Melinis minutiflora*, *Urochloa (Brachiaria) decumbens* and *Setaria sphacelata*) and receives no shading from nearby trees.

The two lowland sites, DRO and Cow Bay are both located within the Daintree Rainforest and as such are similar both geographically and climatically. They differ primarily in soil nutrient status. The upland site Thiaki provides a climate contrast with MAT differing by  $\sim 5.5$  degC and MAP differing by  $\sim 969$  mm compared to the two lowland sites but does not suffer in terms of soil nutrient availability like the Cow Bay site. Comparison of tree performance across these three sites allows assessment of the effects of both climatic (upland vs lowland sites) and edaphic factors (low nutrient vs high nutrient sites).

## 2.2 Study species and plant material

We selected 16 tropical rainforest tree species (Figure 1, Table S1, Figure S1) that are commonly used in revegetation plantings in the Australian Wet Tropics bioregion (Engert *et al.* 2020), taxonomically diverse (representing 13 families), and exhibit a broad range of plant functional traits and successional strategies (Goosem & Tucker 2013). Plant material with verified coordinates or collection location descriptions were sourced from local nurseries including Cairns Regional Council, Rainforest Rescue, Douglas Shire Council, Tablelands Regional Council, and Kuranda Envirocare. For each species, we obtained 30 individual seedlings from either lowland or upland origin ( $n = 960 = 30$  seedlings  $\times$  2 provenance  $\times$  16 species). For two species (*Davidsonia pruriens* and *Syzygium kuranda*) only 15 seedlings could be sourced from a single upland maternal location so seedlings from an additional upland maternal location were included to make up the 30 total replicate seedlings needed (Table S1). During seedling handling and planting, we made sure plant provenance could be tracked back to the maternal plant location, however for this study we consider any plants originating from above 300 m a.s.l to be of ‘upland provenance’ and any plants originating from below this threshold to be of ‘lowland’ provenance in downstream analyses.

Across the focal species, the lowland and upland provenances differed in their MAT by on average 4.0 degC (range 1.8 to 5.8 degC) and by 836 mm in their MAP (range 102 to 1890 mm) (Table S1). Lowland and upland provenance collection locations were on average 105 km (range 52 to 150 km) apart (great-circle distance calculated with ‘geosphere’ package (Hijmans 2022)), with Lowland provenances sourced from the Daintree Rainforest and upland provenances sourced from the Atherton tablelands (with few exceptions). As such, the comparison between DRO and Thiaki planting sites represented a reciprocal transplant for many species.

## 2.3 Experiment setup and site maintenance

Before planting, each site was treated with a broad-spectrum herbicide (Roundup, active ingredient Glyphosate, SpecialistSales, Toowoomba, QLD, Australia) across the entire plot for the DRO and Cow Bay, or along the planting strips ( $\sim 1$ m wide) across the slope at Thiaki. Saplings  $\sim 6$  to 12 months (mean height 37 cm, range 5 to 107 cm) were planted at each of the three trial sites in late March to April 2022 at 3 m  $\times$  3 m spacing to provide for an even light environment as plants grew. This included ten replicate saplings each of the two provenances (lowland and upland) for 16 species planted at each of the three trial sites ( $n = 320$  at each site). The order of plants was randomised within ‘blocks’ with 1 replicate plant from each of 16 species and provenance (upland or lowland) represented in each block ( $n = 32$  plants per block  $\times$  10 blocks at each site). At planting, soil cores were augered (diameter 200mm, depth  $\sim 30$  cm) with each hole receiving 50g of an organic fertilizer pellet (Organic Life, Terra Firma fertilizers, Beaudesert Qld, Australia), and the

pre-soaked plants replanted and watered in immediately. At the Thiaki site, there was a lack of significant rainfall in the weeks immediately after planting, so seedlings were hand-watered every 3 days until the first rains. After seedling establishment, weed management consisted of periodic row spraying with a C<sub>4</sub>-targeted herbicide (Fuzilade Forte 128C, active ingredient Fluzafop-p, SpecialistSales, Toowoomba, QLD, Australia).

## Measurements of growth and survival

Two months after the initial planting 98.4% survival was observed across all sites. Supplementary planting of additional replicates was carried out to maintain the complete planting matrix; these replacement plants were not included in our survival analyses. Over the experiment, total plant height (m) and plant health (described below) were recorded: at planting, and 4, 12, 17, and 24 months after planting. For multi-stemmed individuals, the total height of the leading stem was measured. Health was assessed qualitatively using an index of 0 to 5, with 0 = dead, 1 = main stem dead but with resprouting evident, and levels 2 to 5 representing; <25%, 25 to 50%, 50 to 75%, and plants with a health class of 1 or lower were classified as functionally dead. For analysis of height data, all functionally dead individuals were excluded.

To account for potential within-site variation in environmental conditions (i.e. edaphic or light conditions) known to impact tree growth across the experimental sites (Cheesman *et al.* 2018) we tested for spatial autocorrelation present in the tree growth rates, using Moran’s I. This test indicated significant spatial autocorrelation in growth data within each plot. As trees were not grouped by species in the plots, this autocorrelation is likely due to intra-site variation in soil properties such as rockiness or fertility. Therefore, to account for this spatial autocorrelation, we built a spatial autologistic term (Dormann 2007) using height data from the August 2023 campaign normalised for each site. We generated autologistic terms using focal windows with diameters of three, five, and seven trees, then selected the window size that addressed spatial autocorrelation while exerting the least influence on the model. All three autologistic terms accounted for spatial autocorrelation in model residuals, thus, we chose the term with a focal diameter of seven trees as it had the least influence on the model and was least likely to bias model parameter estimates (Figure S2).

## 2.4 Common Garden soil and meteorological data

Across each site, nine surface soil samples (0 to 10 cm) were taken for basic physiochemical and nutrient analysis to characterize soil nutrient availability and water-holding capacity (Table S2). In addition, actual site meteorological conditions (rainfall, and daily minimum and maximum temperatures) over the entire experimental period (Figure 2) were extracted from SILO climate database hosted by the Queensland Department of Environment, Science and Innovation (<https://www.longpaddock.qld.gov.au>). Average climatological data (1980 to 2010) for planting sites and seed provenances were taken from CHELSA-BIOCLIM V2.1 dataset (Karger *et al.* 2017, 2018).

## 2.5 Wood density

To explore whether species with different life-history strategies differ in their provenance differentiation, we examined the impact of species wood density, as an important component and continuous variable in the *slow-fast* life-history continuum (Reich 2014). We assume that species with higher wood density generally grow more slowly, have longer lifespans, and exhibit lower mortality rates (Chave *et al.* 2009, Liang *et al.* 2021). We retrieved wood density values for each species from the global wood density database using the ‘BIOMASS’ package v.2.1.8 (Rejou-Mechain *et al.* 2017). Although wood density data for Australian rainforest species are generally sparse, with many species having only one or a few data points, (Preece *et al.* 2015, Ilic *et al.* 2000), we were able to extract species level averages of wood density for all species based on a sample size of 6 individuals on average (range 1 to 46). Given our interest in using this trait as an index of inherent species differences in life history strategies, we considered the data appropriate for our needs.

## 2.6 Data analysis

For each species, we analysed three performance metrics that have fitness consequences: overall survival, height increase after DRO, and Thiaki respectively), and the inherent growth rate. Analysis was limited to just 17 months given a) partial canopy closure by some trees at the DRO was beginning to lead to neighbour

shading b) this allowed us to exclude the impacts of ex-Tropical Cyclone Jasper, which made landfall close to the DRO and Cow Bay sites on the 13<sup>th</sup> Dec 2023 causing extensive regional flooding.

Probability of survival was assessed using a generalised linear model with a binomial response with a ‘log-link’ family. Survival data (1 = alive, 0 = dead) was the response variable. To identify the impact of provenance and site on growth for each species, we fitted a generalised linear model with a Gaussian distribution. We ran parallel analyses of absolute fitness (growth increment over ~17 months) as well as the inherent growth rate (Stanton & Thiede 2005, Lamont *et al.* 2023),  $IGR = \ln\Delta H / \ln H$ , where  $\Delta H$  is the change in height and  $H$  is the initial height. For each model, we looked at the interaction effects of provenance (factor, two levels) and site (factor, three levels), and included covariates for initial height (numeric, continuous) and the underlying spatial autocorrelation as the autologistic term (numeric, continuous) (Dormann 2007).

To determine if species-level wood density could explain the strength and direction of local adaptation, we performed ordinary least squares regression with wood density as the independent variable and local adaptation as the dependent variable. Local adaptation was calculated as the difference between fitness in sympatry and in allopatry averaged across the three sites (Blanquart *et al.* 2013), with local adaptation present if fitness in sympatry is higher than in allopatry. Fitness of each population at each site was derived from the estimated marginal means of either survival probability, height increment, or inherent growth rate from the analyses described above. All analyses were performed using R Statistical Software (R Core Team 2022).

Two species – *Alstonia scholaris* and *Toona ciliata* – were found to have a complex interaction between initial growth and insect herbivory in that once individuals (irrespective of provenance) obtained a certain size they were subject to devastating insect damage from either an unidentified caterpillar or native Cedar tip moth (*Hypsipyla robusta*) respectively. This damage caused loss of the apical meristem and a reduction in overall height in these species at sites where they first gained a larger height - as such these species were excluded from growth analyses (but retained in survival analyses).

## RESULTS

### 3.1 Provenance and site differentiation in tree survival

After 17 months of growth, we had on average 79% survival from the original planting, however, losses were somewhat asymmetric across species. The total explained variance from general linear models on survival ranged from  $R^2 = 0.12$  to 0.69 (mean 0.30) across species. 10/16 species showed significant effects of provenance and/or site on survival, and six showed no effect (Figure 3a, Table 1, Figure S3). In four species, *A. fitzalanii*, *C. ramiflorus*, *G. acutifolia*, and *M. elleryana*, site alone significantly affected survival. In two species (*S. luehmannii*, and *N. dealbata*) provenance alone affected survival: the lowland provenance had a higher survival rate than the upland provenance irrespective of site for each species. For one species (*H. novo-guineensis*), survival was impacted by both provenance and site with no interaction effect (Figure S3). For three species (*C. hypospodia*, *E. grandis*, and *T. ciliata*) there were significant provenance x site effects on survival. In *C. hypospodia* the lowland provenance had higher mean survival at all sites but had greater provenance differentiation at Cow Bay compared to other sites. For *E. grandis*, survival was slightly greater for the upland provenance compared to the lowland provenance when grown at the Cow Bay and Thiaki sites, but the opposite was observed when grown at the DRO site. For *T. ciliata* provenance differentiation was only significant at the DRO site, where the lowland provenance had a higher probability of survival.

### 3.2 Provenance and site patterns in growth

The total explained variance of generalised linear models on growth ranged from  $R^2 = 0.42$  to 0.84 across species. Overall, both site and provenance had strong effects on growth. Across the ~17 months, saplings grew on average 1.0±0.7 and 1.1±0.9 m at Cow Bay and Thiaki respectively but 2.6±1.8 m at the DRO,

with an average growth of some species at the DRO (i.e. *E. grandis*, *H. novoguineensis*, and *T. microcarpa*) being 3b, Table 2, Figure S4), with all species except *N. dealbata* showing significant site effects. All species exhibited greater growth at the DRO site compared to Cow Bay or Thiaki. For five species, provenance had a significant impact on height increment (Figure 3b), and in each species, the lowland provenance was taller than the upland provenance. Only two species (*H. novoguineensis*, *S. kuranda*) showed significant provenance x site effects on height increment, with a greater difference between provenances at the two lowland sites, than at Thiaki.

The strong influence of site was also evident when assessing inherent growth rates, with all but three species (*M. viminalis*, *N. dealbata*, and *S. kuranda*) generally having higher inherent growth rates at the lowland DRO site compared to the upland Thiaki site (Figure 3c, Table 3, Figure S5). When assessing inherent growth rates, a higher proportion of species (8/14) had significant provenance effects, with most of those effects indicating higher inherent growth rate of lowland provenances compared to upland provenances (Figure 3c, Table 3, Figure S5). The exceptions were *M. elleryana*, *S. kuranda*, and *T. microcarpa*, where upland provenances had higher inherent growth rates (except for at the lowland sites in *M. elleryana*).

### 3.3 Wood density effects

The presence and strength of local adaptation (sympatry/allopatry) was significantly associated with species-level wood density for survival ( $R^2 = 0.47$ ,  $P = 0.003$ ), and height increment ( $R^2 = 0.33$ ,  $P = 0.031$ ), but not inherent growth rate ( $R^2 = 0.02$ ,  $P = 0.597$ ) (Figure 4). As a result, species with lower wood density were more likely to display provenance differentiation consistent with local adaptation, whereas species with higher wood density were more likely to be maladapted.

## DISCUSSION

Studies of local adaptation are severely lacking for rainforest tree species that are key to restoration efforts. While meta-analyses are useful to discern drivers of local adaptation in studies across multiple species (Leimu & Fischer 2008, Hereford 2009, Matesanz & Ramirez-Valiente 2019), these studies often vary in methodology, site maintenance and conditions that are not easily accounted for. In this study, we used three common garden sites to investigate the effects of site, provenance, and their interaction on the growth and survival of 16 tree species commonly used in restoration plantings in the Australian Wet Tropics. Site effects were observed in 50% of species for survival, 93% for height increment, and 79% for inherent growth rate. Provenance effects were noted in 38% of species for survival, 36% for height increment, and 57% for inherent growth rate. Interestingly, the lowland provenance generally outperformed the upland provenance regardless of site. We found a negative correlation between species wood density and the magnitude and direction of provenance differentiation (mean sympatric/allopatric comparisons of local adaptation) in both survival and height increment (but not inherent growth rate). This suggests that local adaptation may be more evident in faster-growing species, with no differences or potential maladaptation for slower-growing species, but further monitoring is needed to determine if these preliminary patterns hold. These results challenge the usefulness of a ‘local is best’ provenancing strategy for upland restoration plantings in the Australian Wet Tropics and help to fill the gap in our understanding of the extent of local adaptation in tropical rainforest trees globally.

### 4.1 Site effects on growth and survival

We used three common garden sites to contrast tree performance across two major environmental axes commonly encountered by restoration practitioners: nutrient availability (DRO vs Cow Bay) and climate (DRO vs Thiaki). We found a substantial impact of site on both survival and growth of tropical trees planted under common garden conditions, with trees at the DRO gaining on average over twice the height increment seen at the other two sites. This resulted in the DRO planting site reaching effective site capture and partial canopy closure after 1.5 years of growth with a planting density of just 1100 trees ha<sup>-1</sup>, far lower than the planting density commonly employed in the Australian Wet Tropics (Goosem & Tucker 2013). In contrast, poor overall growth at the Cow Bay site necessitated continued site maintenance. The differences

between the DRO and Cow Bay highlight the significant impact that edaphic context can have on tree growth and restoration success. The DRO and Thiaki sites were not limited in nutrient availability, and differed primarily in climate conditions, with the DRO site experiencing on average higher temperatures, vapour pressure deficit, and rainfall than Thiaki. The higher growth rates observed at the DRO compared to Thiaki are consistent with elevational patterns of growth observed in natural populations across the Australian Wet Tropics (Bradford *et al.* 2014, Bauman *et al.* 2022). This has been linked to warmer temperatures stimulating growth and biomass accumulation in tropical tree species that can be masked or limited by the associated increase in vapour pressure deficit (Smith *et al.* 2020, Middleby *et al.* 2024a). While the contrasting temperatures of the DRO and Thiaki sites likely contributed to the growth differences across these sites, it is also important to note the site differences in precipitation and therefore soil moisture. Although both sites receive relatively high levels of mean annual precipitation, the cumulative rainfall at the DRO was over 2x higher during the study period compared to Thiaki. We therefore cannot rule out the effect that soil moisture may have had on plant performance during this trial.

#### 4.2 Impacts of provenance but mixed evidence for local adaptation

In comparing the growth and survival of upland and lowland provenances between the DRO and Thiaki we had hoped to isolate the impacts of temperature - and given the proximity of maternal populations to planting sites (Figure S1) the prevalence of local adaptation in our study species. Although we found that the lowland provenance often outperformed the upland provenance at the lowland site, we rarely found the reciprocal to be true *i.e.* upland provenances did not outperform lowland provenances in the upland site, indicating a partial lack of local adaptation *sensu* Kawecki and Ebert (2004). Despite this study only including three sites and thus having relatively low power to detect local adaptation (Blanquart *et al.* 2013), many examples supporting our results challenge the notion that this is widespread (Leimu & Fischer 2008, Bucharova *et al.* 2016, Mushagalusa *et al.* 2020). Our findings resemble those observed in the reciprocal transplant of *Quercus oleoides* populations conducted by Deacon & Cavender-Bares (2015). In their study, the lowland provenance also exhibited higher mean fitness at all sites compared to the upland provenance. Given that faster growth rates are typically observed in lowland environments (Bradford *et al.* 2014, Bauman *et al.* 2022), it is possible that lowland populations of rainforest trees generally have evolved higher growth rates than upland populations, potentially at the cost of stress tolerance or other fitness metrics (Willi & Van Buskirk 2022). Another possibility is that the lowland provenance seedlings in our study were sourced from more intact populations with higher reproductive population size and therefore genetic diversity, which has been linked to higher fitness (Reed & Frankham 2003). Confirming this requires further work assessing within-species genetic diversity and differentiation across populations. However, it is possible that upland provenances may possess greater stress tolerance, and a full life-cycle assessment is needed to determine any true differences in population fitness. Furthermore, in Deacon & Cavender-Bares (2015) study, the advantage of the lowland provenance was only temporary with provenance differences no longer evident by the third year, highlighting the importance of continued monitoring of such studies when assessing patterns of local adaptation (Preece *et al.* 2023).

#### 4.3 Stronger provenance effects in fast vs. slow growth species

Provenance trials are highly resource-intensive (Sork *et al.* 2013), often restricting investigations to a single species. However, local adaptation can be highly species- and context-dependent, which limits the broad applicability of climate-matching provenance strategies in tropical systems with high species diversity. We differentiated between species that generally grow slower, live longer, and invest more resources into defences than those that grow fast and have a more rapid lifecycle using the fundamental plant trait wood density (Poorter *et al.* 2008, Wright *et al.* 2010). We found that species-level wood density was negatively associated with the mean performance of provenances grown in sympatry vs those grown for survival and growth (height increment). This supports our hypothesis that faster-growing species with shorter generation times are more likely to exhibit local adaptation, with slower-growing species potentially more likely to be maladapted. However, this was not the case for inherent growth rate. It is likely that after only 1.5 years of measurements, provenance variation is observable primarily in faster-growing species or at sites where resource limitations



do not obscure growth potential, and so it remains unclear whether the observed provenance differences are due to higher rates of molecular evolution in faster-growing species (Smith & Donoghue 2008).

#### 4.4 Conclusions and implications for rainforest restoration in the Australian Wet Tropics

Although site and provenance effects were important in determining tree survival and growth across our 16 study species, evidence for local adaptation was mixed. For most species the lowland provenance performed better than the upland provenance regardless of site, and provenance differences were generally stronger in faster growing species. This highlights the complexity and context-dependency of local adaptation in tropical rainforest trees, challenging the ‘local is best’ strategy for sourcing seed for restoration plantings (Cooper *et al.* 2018). Our findings suggest that using lowland provenances, regardless of site, could optimize initial plant growth in some species. Restoration practitioners might consider expanding the sources of seed, particularly in higher altitude sites like the Atherton Tablelands, to meet seed demands and enhance genetic diversity and adaptive capacity. However, risks associated with both local and mixed provenancing approaches are well-documented (Jordan *et al.* 2024). Future research at this site includes investigating whether observed growth responses evident here can be explained by variation of physiological traits, or whether trade-offs exist with growth and tolerance to heat (Middleby *et al.* 2024b) or drought stress. We urge researchers and practitioners in this region to focus on generating the necessary information for informed decision-making.

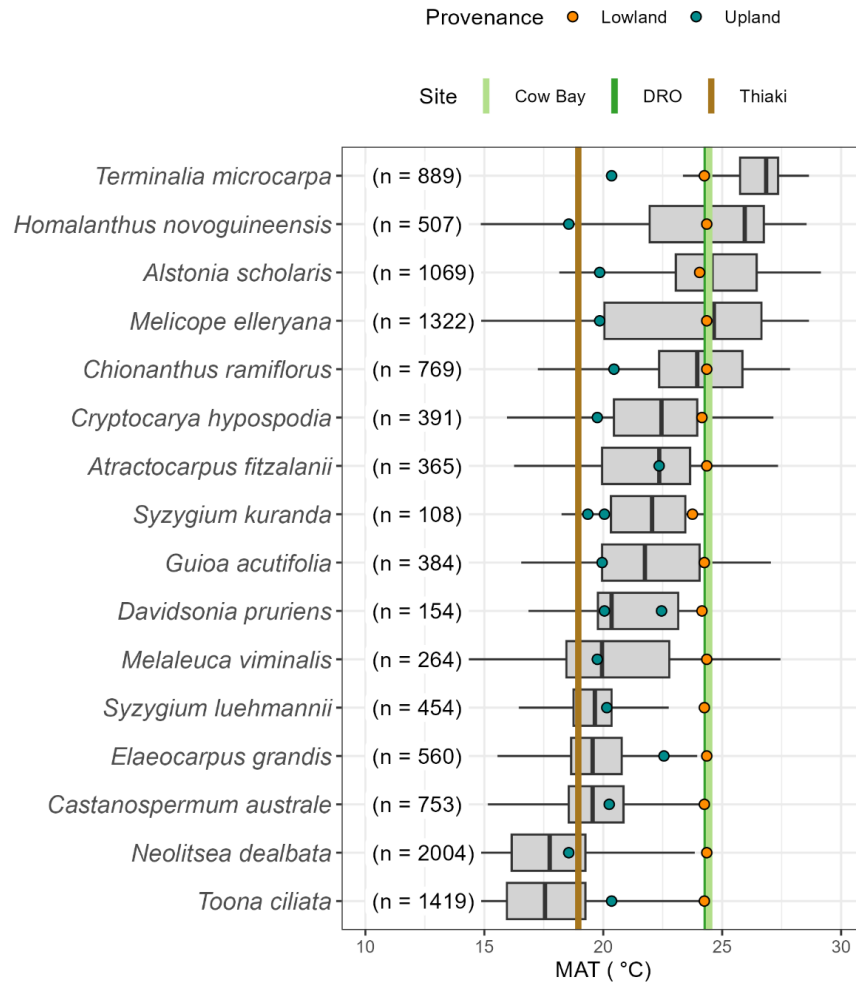


Figure 1. Comparison of mean annual temperature (MAT) of origin for seed source and planting locations within observed thermal niche of each species (GBIF 2024). Boxplots show the MAT (1981-2010 CHELSA database V.2.1) distribution throughout each species global native range (occurrences obtained from GBIF, cleaned for errors, and spatially thinned to 1km resolution). The black line is the median, with the grey filled region equal to  $1.5 \times$  the interquartile range. Whiskers represent the 25<sup>th</sup> and 75<sup>th</sup> percentile, and outliers are not shown for clarity. The red and blue points represent the MAT of origin for the seed source locations of the lowland and upland provenances respectively. The three coloured vertical lines represent the MAT at the common garden sites. Species are arranged in order of their mean thermal niche.

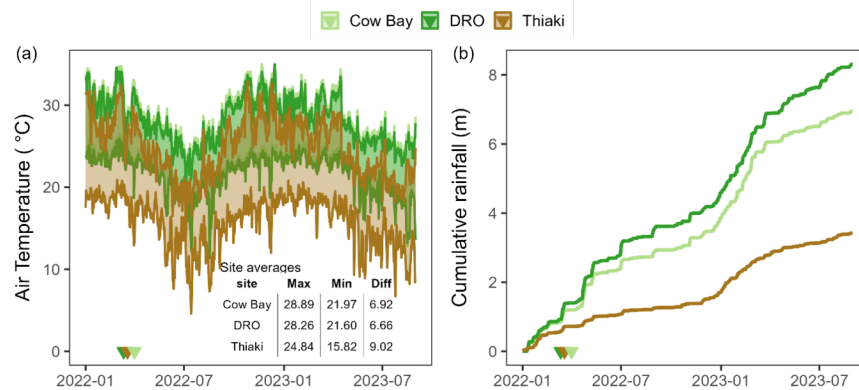


Figure 2. Meteorology at each site during the experiment. Plots show (a) daily max and min air temperature (°C) and (b) cumulative daily rainfall (m) from 01-01-2022 until the last census date 31-08-2023. The triangle points mark the planting dates. Table inset for panel (a) reports the overall means of daily max, min, and difference between max and min (diff) for air temperature (°C) at each site.

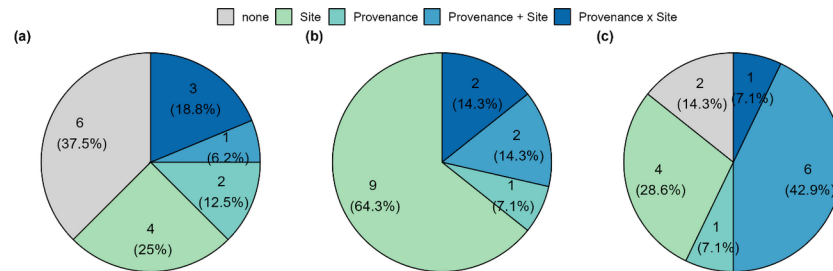


Figure 3. Proportion of species showing significant (including marginal) effects of provenance and site on survival (a) height increment (b) and inherent growth rate (c) in this study. Pie charts show the number and percentage of species that had  $P < 0.1$  for effects of just ‘Site’, just ‘Provenance’, both ‘Site’ and ‘Provenance’, or their interaction ‘Provenance  $\times$  Site’ ( $n = 16$  species for survival and 14 species for growth). For full statistical details see Tables 1, 2, and 3.

Table 1. Effects of provenance and site on survival. Table reports results for Generalized Linear Models on the effect of provenance, site, and their interaction on probability of individual stem survival. Covariates include initial plant height, as well as spatial autocorrelation using a window based upon 7 trees. Binomial distribution was taken as the link function. Results with  $P < 0.1$  are bolded.

Species	Spatial-correlation		Initial Height		Site		Provenance		Provenance × Site	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Alstonia scholaris</i>	1.12	0.289	3.87	<b>0.049</b>	2.85	0.241	0			
<i>Atractocarpus fitzalanii</i>	0.02	0.88	1.89	0.169	7.29	<b>0.026</b>	1			
<i>Castanospermum australe</i>	0.13	0.717	2.16	0.142	3.88	0.144	2			
<i>Chionanthus ramiflorus</i>	3.12	<b>0.077</b>	2.91	<b>0.088</b>	18.00	< <b>0.0001</b>	2			
<i>Cryptocarya hypospodia</i>	4.41	<b>0.036</b>	1.52	0.217	22.03	< <b>0.0001</b>	2			
<i>Davidsonia pruriens</i>	3.98	<b>0.046</b>	3.76	<b>0.053</b>	1.81	0.405	0			
<i>Elaeocarpus grandis</i>	1.61	0.204	1.32	0.251	1.68	0.432	0			
<i>Guioa acutifolia</i>	3.50	<b>0.061</b>	3.60	<b>0.058</b>	12.68	<b>0.002</b>	8			
<i>Homalanthus novoguineensis</i>	11.32	<b>0.001</b>	6.20	<b>0.013</b>	13.40	<b>0.001</b>	4			
<i>Melaleuca viminalis</i>	1.57	0.21	0.48	0.487	4.09	0.129	0			
<i>Melicope elleryana</i>	2.22	0.136	2.14	0.143	8.01	<b>0.018</b>	0			
<i>Neolitsea dealbata</i>	2.47	0.116	1.10	0.294	2.65	0.266	1			
<i>Syzygium kuranda</i>	4.70	<b>0.03</b>	0.77	0.38	1.61	0.446	0			
<i>Syzygium luehmannii</i>	3.49	<b>0.062</b>	0.02	0.884	2.69	0.261	3			
<i>Terminalia microcarpa</i>	5.75	<b>0.016</b>	0.68	0.409	1.43	0.49	0			
<i>Toona ciliata</i>	0.84	0.361	1.31	0.252	1.65	0.437	4			

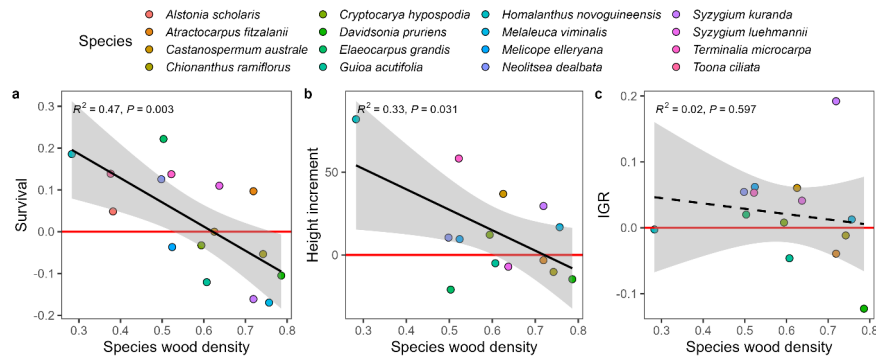
Table 2. Table of model on the effect of provenance and site and their interaction on incremental growth in tree heights using glm with gaussian distribution. Covariates include initial plant height and spatial autocorrelation. Spatial autocorrelation taken into account as a covariate (Spatial) using a window based upon 7 trees. Results with  $P < 0.1$  are bolded.

Species	Spatial-correlation		Initial Height		Site		Provenance		Provenance × Site		$R^2$
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
<i>Atractocarpus fitzalanii</i>	6.96	<b>0.008</b>	0.84	0.359	79.88	< <b>0.0001</b>	1				
<i>Castanospermum australe</i>	5.50	<b>0.019</b>	0.03	0.875	55.48	< <b>0.0001</b>	1				
<i>Chionanthus ramiflorus</i>	5.46	<b>0.0195</b>	0.96	0.328	9.68	<b>0.008</b>	0				
<i>Cryptocarya hypospodia</i>	18.75	< <b>0.0001</b>	0.04	0.839	10.40	<b>0.006</b>	1				
<i>Davidsonia pruriens</i>	5.64	<b>0.018</b>	2.80	<b>0.095</b>	39.08	< <b>0.0001</b>	0				
<i>Elaeocarpus grandis</i>	28.55	< <b>0.0001</b>	3.02	<b>0.082</b>	46.66	< <b>0.0001</b>	2				
<i>Guioa acutifolia</i>	2.80	<b>0.094</b>	0.68	0.411	9.10	<b>0.011</b>	1				
<i>Homalanthus novoguineensis</i>	20.11	< <b>0.0001</b>	0.77	0.381	94.27	< <b>0.0001</b>	2				
<i>Melaleuca viminalis</i>	3.45	<b>0.063</b>	0.99	0.320	14.94	<b>0.0006</b>	1				
<i>Melicope elleryana</i>	29.37	< <b>0.0001</b>	0.27	0.603	104.2	< <b>0.0001</b>	1				
<i>Neolitsea dealbata</i>	23.45	< <b>0.0001</b>	0.14	0.710	4.30	0.116	4				
<i>Syzygium kuranda</i>	0.08	0.781	1.89	0.170	9.86	<b>0.007</b>	0				
<i>Syzygium luehmannii</i>	3.98	<b>0.046</b>	0.45	0.505	13.19	<b>0.001</b>	0				
<i>Terminalia microcarpa</i>	1.28	0.257	0.56	0.454	51.15	< <b>0.0001</b>	0				

Table 3. Table of model on the effect of provenance and site and their interaction on inherent growth rate in tree heights using glm with gaussian distribution. Spatial autocorrelation taken into account as a covariate using a window based upon 7 trees. Results with  $P < 0.1$  are bolded.

Species	Spatial-correlation		Site	Provenance	Provenance × Site	$R^2$	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>
<i>Atractocarpus fitzalanii</i>	6.587	<b>0.0103</b>	64.392	< <b>0.0001</b>	0.613	0.4338	1.8

Species	Spatial-correlation	Site	Provenance	Provenance × Site	$R^2$		
<i>Castanospermum australe</i>	6.75	<b>0.0094</b>	33.828	<b>&lt;0.0001</b>	2.402	0.1212	1.5
<i>Chionanthus ramiflorus</i>	1.009	0.3151	9.066	<b>0.0107</b>	0.003	0.9581	0.0
<i>Cryptocarya hypospodia</i>	22.189	<b>&lt;0.0001</b>	4.912	<b>0.0858</b>	17.073	<b>&lt;0.0001</b>	0.0
<i>Davidsonia pruriens</i>	7.441	<b>0.0064</b>	18.19	<b>0.0001</b>	18.038	<b>&lt;0.0001</b>	1.8
<i>Elaeocarpus grandis</i>	12.527	<b>0.0004</b>	12.282	<b>0.0022</b>	19.176	<b>&lt;0.0001</b>	0.2
<i>Guioa acutifolia</i>	2.993	<b>0.0836</b>	5.354	<b>0.0688</b>	60.12	<b>&lt;0.0001</b>	0.4
<i>Homalanthus novoguineensis</i>	11.576	<b>0.0007</b>	43.694	<b>&lt;0.0001</b>	42.983	<b>&lt;0.0001</b>	0.1
<i>Melaleuca viminalis</i>	1.119	0.2902	1.775	0.4117	0.665	0.4149	0.1
<i>Melicope elleryana</i>	10.299	<b>0.0013</b>	44.376	<b>&lt;0.0001</b>	3.671	<b>0.0554</b>	5.8
<i>Neolitsea dealbata</i>	6.695	<b>0.0097</b>	0.346	0.8409	1.184	0.2766	2.1
<i>Syzygium kuranda</i>	0.124	0.7244	1.652	0.4378	3.152	<b>0.0758</b>	3.6
<i>Syzygium luehmannii</i>	1.013	0.3142	6.271	<b>0.0435</b>	0.29	0.5899	0.4
<i>Terminalia microcarpa</i>	1.171	0.2792	19.237	<b>&lt;0.0001</b>	10.95	<b>0.0009</b>	1.0



**Figure 4:** Relationship between species-level wood density and population differentiation for survival (a) height increment (b) and inherent growth rate, IGR (c) in tropical trees grown across three common garden experimental plots. All points represent the sympatric/allopatric calculations of local adaptation using pairwise comparisons for lowland and upland provenances from the models. Values greater than 0 (red horizontal line) indicate greater mean performance of the local provenance in their local site (local adaptation), and values  $< 0$  indicate greater mean performance of the nonlocal provenance in their nonlocal sites (maladaptation), significant regression trends ( $P < 0.05$ ) are indicated by solid line.

## ACKNOWLEDGEMENTS

We would like to thank Marine Deliens, and Allen Sheather from Rainforest Rescue, and Michele Schifer, Andrew Thomson, and Johan Larson from the Daintree Rainforest Observatory for logistical support during the set up and maintenance of plots. We also thank our nursery contacts for providing us with the plant material for this experiment including Ryan Zihrul from Cairns Council Nursery, Marine Deliens from Rainforest Rescue, Gaylene Sheather from Douglas Shire Council Nursery, Audrey Hill at Tablelands Regional Council, and Cathy Retter at Kuranda Envirocare. Thanks to the volunteers who helped with the initial tree planting and measurement campaigns. This work was funded by the Australian Research Council project “LP190100484” and is a further contribution to Australian Research Council Linkage project LP0989161.

## Author Contribution Statement

**KM:** Conceptualization, investigation, analysis, visualisation, writing – original draft; **LC, MB, DC, & SL:** Funding acquisition, conceptualisation; **NP & Pvo:** Conceptualisation, resources; **JE:** Resources; **AC:** Project administration, funding acquisition, conceptualisation, analysis, investigation. All authors contributed to final writing – reviewing and editing.

### SUPPLEMENTARY INFORMATION

Table S1. Provenance information for species used in study. Mean annual temperature (MAT, °C) and precipitation (MAP, mm) from between 1980 and 2010 as retrieved from CHELSA V2.1 (Karger *et al.* 2017, 2018). Letters in brackets within the provenance column denote separate information for species whose upland population was collected from two different locations. Latitude and Longitude are given in decimal degrees.

Species	Provenance	Latitude	Longitude	Locality	MAT (°C)	MAP (mm)
<i>Alstonia scholaris</i> (Apocynaceae)	lowland	-16.8295	145.7023	Smithfield	24.1	195
	upland	-17.2893	145.6177	Yungaburra	19.9	242
<i>Atractocarpus fitzalanii</i> (Rubiaceae)	lowland	-16.2029	145.4041	Diwan	24.4	307
	upland	-16.8493	145.6208	Kuranda	22.4	178
<i>Castanospermum australe</i> (Fabaceae)	lowland	-16.4725	145.3649	Mossman	24.3	229
	upland	-17.3359	145.5003	Wongabel	20.3	189
<i>Chionanthus ramiflorus</i> (Oleaceae)	lowland	-16.2029	145.4041	Diwan	24.4	307
	upland	-17.2742	145.5805	Yungaburra	20.5	206
<i>Cryptocarya hypospodia</i> (Lauraceae)	lowland	-16.2377	145.4279	Cow Bay	24.2	295
	upland	-17.3687	145.6746	Glen Allyn	19.8	309
<i>Davidsonia pruriens</i> (Cunoniaceae)	lowland	-16.2382	145.4324	Cow Bay	24.2	295
	upland (a)	-17.3550	145.5878	Malanda	20.1	244
	upland (b)	-16.8069	145.5806	Kuranda	22.5	165
<i>Elaeocarpus grandis</i> (Elaeocarpaceae)	lowland	-16.1770	145.4128	Diwan	24.4	333
	upland	-16.8053	145.6140	Kuranda	22.6	179
<i>Guioa acutifolia</i> (Sapindaceae)	lowland	-16.2620	145.3337	Daintree	24.3	235
	upland	-17.3090	145.6137	Peeramon	20.0	245
<i>Homalanthus novoguineensis</i> (Euphorbiaceae)	lowland	-16.1770	145.4128	Diwan	24.4	333
	upland	-17.5205	145.5679	Milla Milla	18.6	287
<i>Melaleuca viminalis</i> (Myrtaceae)	lowland	-16.1770	145.4128	Diwan	24.4	333
	upland	-17.3703	145.3904	Herberton	19.8	144
<i>Melicope elleryana</i> (Rutaceae)	lowland	-16.1770	145.4128	Diwan	24.4	333
	upland	-17.2995	145.4585	Carrington	19.9	166
<i>Neolitsea dealbata</i> (Lauraceae)	lowland	-16.1770	145.4128	Diwan	24.4	333
	upland	-17.5202	145.5691	Milla Milla	18.6	287
<i>Syzygium kuranda</i> (Myrtaceae)	lowland	-16.2344	145.4485	Cow Bay	23.8	302
	upland (a)	-17.3548	145.5861	Malanda	20.1	244
	upland (b)	-16.2775	145.0675	Mt Windsor	19.4	170
<i>Syzygium luehmannii</i> (Myrtaceae)	lowland	-16.4725	145.3649	Mossman	24.3	229
	upland	-17.2769	145.4925	Atherton	20.2	170
<i>Terminalia microcarpa</i> (Combretaceae)	lowland	-16.2620	145.3337	Daintree	24.3	235
	upland	-17.2628	145.4817	Atherton	20.4	160
<i>Toona ciliata</i> (Meliaceae)	lowland	-16.4725	145.3649	Mossman	24.3	229
	upland	-17.2397	145.4801	Tolga	20.4	153

Table S2. Surface soil characteristics for the three common garden sites.

Site	DRO	Cow Bay	Thiaki
Soil Organic matter <sup>1</sup> (%)	16.58 ±	1.99	8.43 ± 1.44
Total Carbon <sup>2</sup> (mg g <sup>-1</sup> )	51.89 ±	6.49	26.38 ± 6.84
Total Nitrogen <sup>2</sup> (mg g <sup>-1</sup> )	4.32 ±	0.61	2.16 ± 0.73
pH <sup>3</sup>	5.23 ±	0.11	5.20 ± 0.15
CEC <sup>4</sup> (cmol <sup>+</sup> kg <sup>-1</sup> )	3.12 ±	0.65	1.55 ± 0.17
Available K (µg g <sup>-1</sup> )	71.22 ±	12.30	32.63 ± 8.12
Total Phosphorus (µg g <sup>-1</sup> )	873.33 ±	151.58	297.50 ± 39.91

<sup>1</sup> determined by Loss on ignition (550°C, 4h)

<sup>2</sup> determined by Elemental Analysis

<sup>3</sup> pH determined in 1:5 DDI water

1. Cation Exchange capacity determined using ammonium acetate method, all base cations including aluminium
2. Available potassium determined using ammonium acetate
3. Total phosphorus determined after acid digestion and ICP-OES analysis

Figure S1. Map of trial sites and seed collection locations for each species in the Wet Tropics Bioregion of Australia. Sites represented by black squares. Provenance locations for each species represented with coloured circles.

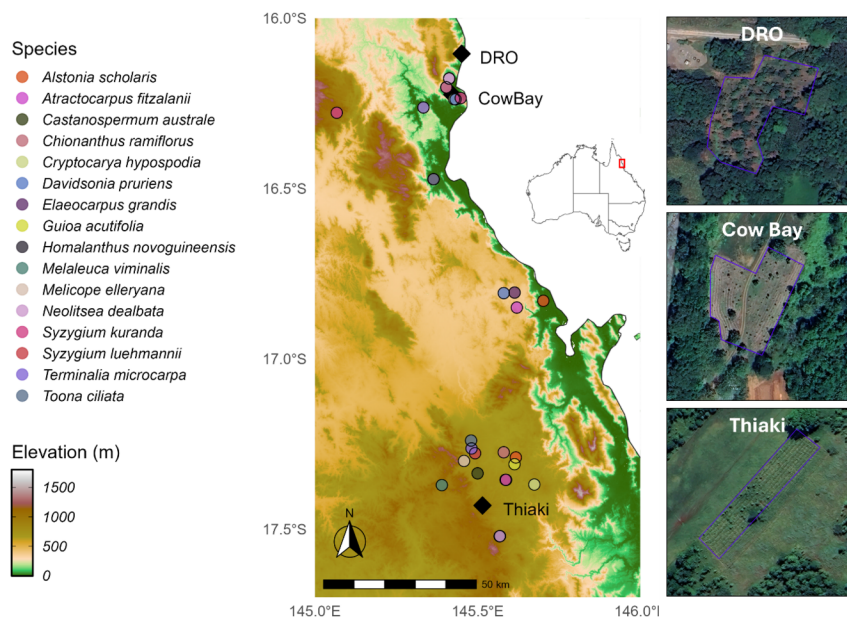


Figure S2: Map of spatial autocorrelation term built using a focal window of seven trees and used in the final model to account for spatial autocorrelation in observed growth rates across the three planting sites.

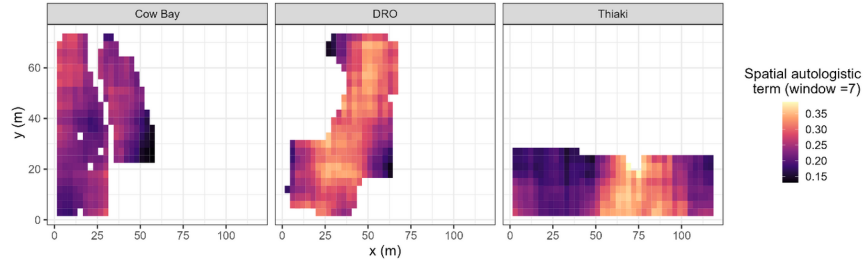


Figure S3: Proportion of planted saplings of 16 tropical tree species surviving to 1.5 years in one of three common garden planting sites in the Australian Wet Tropics. Points represent estimated marginal means of survival accounting for spatial correlation from full model (see text) for each species with lines indicating confidence interval.

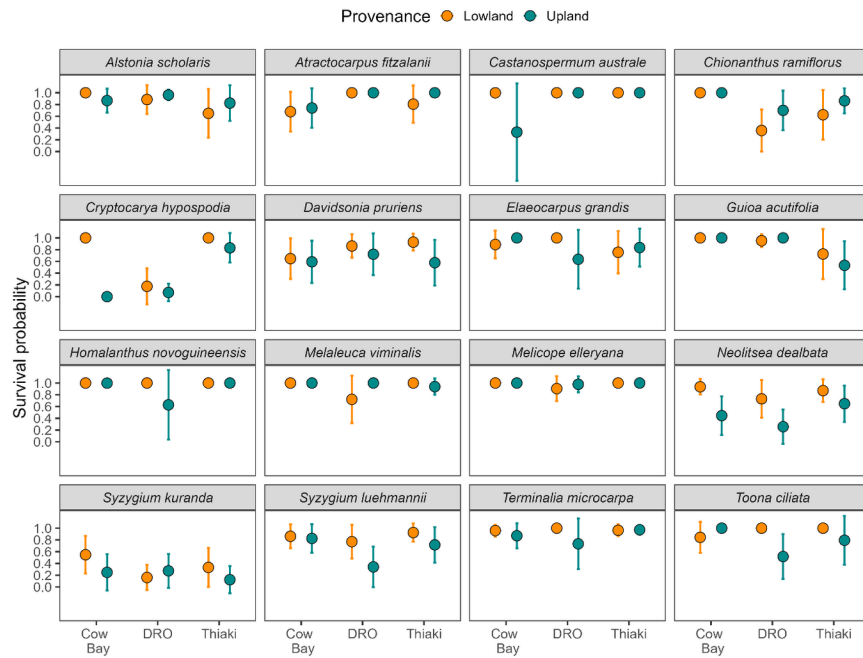


Figure S4. Growth increment across ~17 months in all surviving plants of 14 tropical tree species grown under three common garden conditions in the Australian Wet Tropics. Points represent estimated marginal means of absolute growth increment from full models (see text) for each species with lines indicating confidence interval. Note two species (*Alstonia scholaris* and *Toona ciliata*) removed from analysis given complex interaction with herbivory (see text).

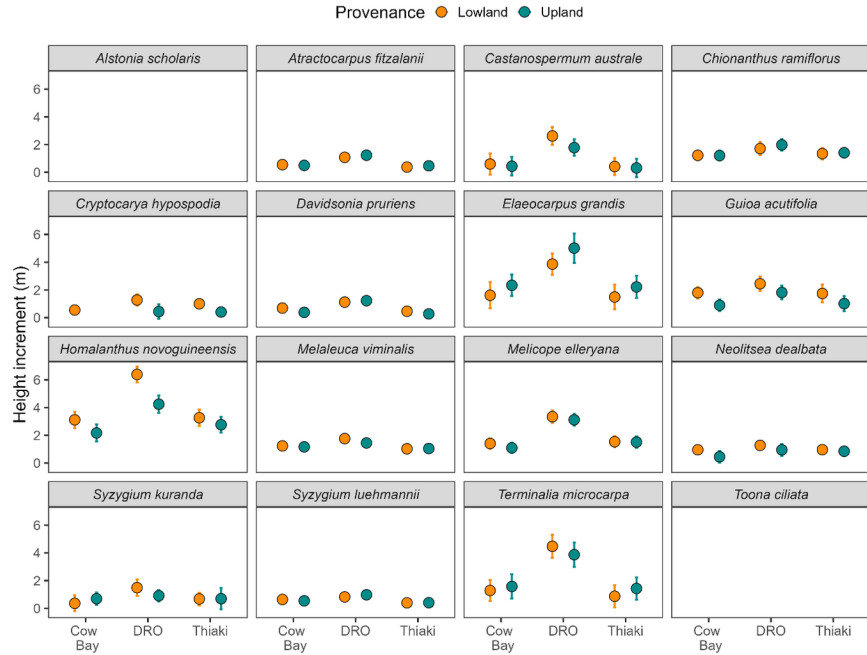
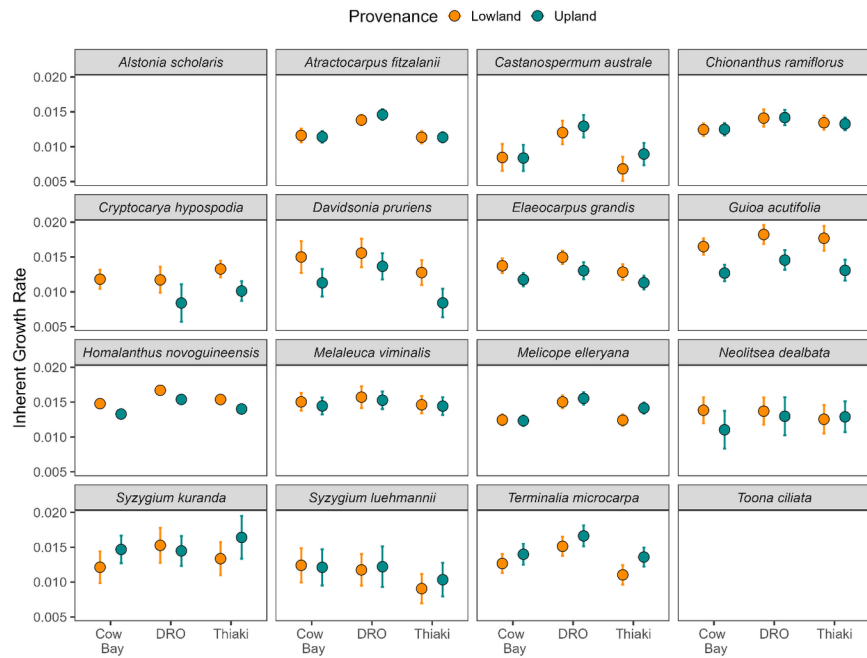


Figure S5. Inherent growth rate across ~17 months in all surviving plants of 14 tropical tree species grown under three common garden conditions in the Australian Wet Tropics. Points represent estimated marginal means of inherent growth rate from full models (see text) for each species with lines indicating confidence interval. Note two species (*Alstonia scholaris* and *Toona ciliata*) removed from analysis given complex interaction with herbivory (see text)





## References

- Aitken, S. N., and M. C. Whitlock. 2013. Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. *In* D. J. Futuyma (Ed.). *Annual Review of Ecology, Evolution, and Systematics*, Vol 44. Annual Reviews, Palo Alto.
- Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Avila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. a. M. Mestre, R. Miranda-Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. Da Silva, C. D. Motta, and C. A. Peres. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* , **104** , 18555-18560.
- Bauman, D., C. Fortunel, L. A. Cernusak, L. P. Bentley, S. M. McMahon, S. W. Rifai, J. Aguirre-Gutiérrez, I. Oliveras, M. Bradford, S. G. W. Laurance, G. Delhaye, M. F. Hutchinson, R. Dempsey, B. E. Mcnellis, E. Santos-Andrade, Paul, H. R. Ninantay-Rivera, J. R. Chambi Paucar, O. L. Phillips, and Y. Malhi. 2022. Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits. *Global Change Biology* , **28** , 1414-1432.
- Blanquart, F., O. Kaltz, S. L. Nuismer, and S. Gandon. 2013. A practical guide to measuring local adaptation. *Ecology Letters* ,**16** , 1195-1205.
- Bradford, M. G., H. T. Murphy, A. J. Ford, D. L. Hogan, and D. J. Metcalfe. 2014. Long-term stem inventory data from tropical rain forest plots in Australia. *Ecology* , **95** , 2362-2362.
- Brancalion, P. H. S., G. C. X. Oliveira, M. I. Zucchi, M. Novello, J. Van Melis, S. S. Zocchi, R. L. Chazdon, and R. R. Rodrigues. 2018. Phenotypic plasticity and local adaptation favor range expansion of a Neotropical palm. *Ecology and Evolution* , **8** , 7462-7475.
- Breed, M. F., M. G. Stead, K. M. Ottewell, M. G. Gardner, and A. J. Lowe. 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* ,**14** , 1-10.
- Bucharova, A., W. Durka, J. M. Hermann, N. Holzel, S. Michalski, J. Kollmann, and O. Bossdorf. 2016. Plants adapted to warmer climate do not outperform regional plants during a natural heat wave. *Ecology and Evolution* , **6** , 4160-4165.
- Charles, L. S., J. M. Dwyer, T. J. Smith, S. Connors, P. Marschner, and M. M. Mayfield. 2018. Seedling growth responses to species-, neighborhood-, and landscape-scale effects during tropical forest restoration. *Ecosphere* , **9** , e02386.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* , **12** , 351-366.
- Cheesman, A. W., N. D. Preece, P. Van Oosterzee, P. D. Erskine, and L. A. Cernusak. 2018. The role of topography and plant functional traits in determining tropical reforestation success. *Journal of Applied Ecology* , **55** , 1029-1039.
- Colwell, R. K., and K. J. Feeley. 2024. Still little evidence of poleward range shifts in the tropics, but lowland biotic attrition may be underway. *Biotropica* , e13358.
- Cooper, S. L., C. Catterall, and P. C. Bundock. 2018. Local provenancing in subtropical rainforest restoration: For better or worse? A review of practitioners' perspectives. *Ecological Management & Restoration* , **19** , 156-165.
- Cordero, I., M. D. Jimenez, J. A. Delgado, L. Balaguer, J. J. Pueyo, and A. Rincon. 2021. Local adaptation optimizes photoprotection strategies in a Neotropical legume tree under drought stress. *Tree Physiology* , **41** , 1641-1657.

- Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* , **28** , 482-488.
- Deacon, N. J., and J. Cavender-Bares. 2015. Limited Pollen Dispersal Contributes to Population Genetic Structure but Not Local Adaptation in *Quercus oleoides* Forests of Costa Rica. *Plos One* , **10** .
- Degen, B., and A. Sebbenn. 2015. Genetics and Tropical Forests. *In* L. Pancel and M. Kohl (Eds.). *Tropical Forestry Handbook*, pp. 885-920. Springer Nature, Heidelberg.
- Derived dataset GBIF.org (17 July 2024) Filtered export of GBIF occurrence data <https://doi.org/10.15468/dd.a4mjzn>.
- Dormann, C. F. 2007. Assessing the validity of autologistic regression. *Ecological Modelling* , **207** , 234-242.
- Doughty, C. E., J. M. Keany, B. C. Wiebe, C. Rey-Sanchez, K. R. Carter, K. B. Middleby, A. W. Cheesman, M. L. Goulden, H. R. Da Rocha, S. D. Miller, Y. Malhi, S. Fauset, E. Gloor, M. Slot, I. Oliveras Menor, K. Y. Crous, G. R. Goldsmith, and J. B. Fisher. 2023. Tropical forests are approaching critical temperature thresholds. *Nature* , **621** , 105-111.
- Engert, J. E., N. O. Vogado, K. Freebody, B. Byrne, J. Murphy, G. Sheather, P. Snodgrass, L. Nugent, D. Lloyd, and S. G. W. Laurance. 2020. Functional trait representation differs between restoration plantings and mature tropical rainforest. *Forest Ecology and Management* , **473** , 9.
- Friedlingstein, P., M. W. Jones, M. O'sullivan, R. M. Andrew, D. C. E. Bakker, J. Hauck, C. Le Quere, G. P. Peters, W. Peters, J. Pongratz, S. Sitch, J. G. Canadell, P. Ciais, R. B. Jackson, S. R. Alin, P. Anthoni, N. R. Bates, M. Becker, N. Bellouin, L. Bopp, T. T. T. Chau, F. Chevallier, L. P. Chini, M. Cronin, K. I. Currie, B. Decharme, L. M. Djeutchouang, X. Y. Dou, W. Evans, R. A. Feely, L. Feng, T. Gasser, D. Gilfillan, T. Gkritzalis, G. Grassi, L. Gregor, N. Gruber, O. Gurses, I. Harris, R. A. Houghton, G. C. Hurtt, Y. Iida, T. Ilyina, I. T. Lujikx, A. Jain, S. D. Jones, E. Kato, D. Kennedy, K. K. Goldewijk, J. Knauer, J. I. Korsbakken, A. Kortzinger, P. Landschutzer, S. K. Lauvset, N. Lefevre, S. Lienert, J. J. Liu, G. Marland, P. C. Mcguire, J. R. Melton, D. R. Munro, J. Nabel, S. I. Nakaoka, Y. Niwa, T. Ono, D. Pierrot, B. Poulter, G. Rehder, L. Resplandy, E. Robertson, C. Rodenbeck, T. M. Rosan, J. Schwinger, C. Schwingshackl, R. Seferian, A. J. Sutton, C. Sweeney, T. Tanhua, P. P. Tans, H. Q. Tian, B. Tilbrook, F. Tubiello, G. R. Van Der Werf, N. Vuichard, C. Wada, R. Wanninkhof, A. J. Watson, D. Willis, A. J. Wiltshire, W. P. Yuan, C. Yue, X. Yue, S. Zaehle, and J. Y. Zeng. 2022. Global Carbon Budget 2021. *Earth System Science Data* , **14** , 1917-2005.
- Gbif. 2024. Derived dataset GBIF.org (17 July 2024) Filtered export of GBIF occurrence data <https://doi.org/10.15468/dd.a4mjzn> *In* A. Cheesman (Ed.).
- Gellie, N. J. C., M. F. Breed, N. Thurgate, S. A. Kennedy, and A. J. Lowe. 2016. Local maladaptation in a foundation tree species: Implications for restoration. *Biological Conservation* , **203** , 226-232.
- Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* , **478** , 378-+.
- Girardin, C. a. J., S. Jenkins, N. Seddon, M. Allen, S. L. Lewis, C. E. Wheeler, B. W. Griscom, and Y. Malhi. 2021. Nature-based solutions can help cool the planet - if we act now. *Nature* , **593** , 191-194.
- Goosem, S., and N. Tucker. 2013. Repairing the Rainforest Wet Tropics Management Authority, Cairns, Queensland, Australia, & Biotropica Australia, Tarzali, Queensland, Australia.
- Hammond, W. M., A. P. Williams, J. T. Abatzoglou, H. D. Adams, T. Klein, R. Lopez, C. Saenz-Romero, H. Hartmann, D. D. Breshears, and C. D. Allen. 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* , **13** .

- Hereford, J. 2009. A Quantitative Survey of Local Adaptation and Fitness Trade-Offs. *The American Naturalist* , **173** , 579-588.
- Hijmans, R. J. 2022. geosphere: Spherical Trigonometry.
- Jordan, R., P. Harrison, and M. Breed. 2024. The eco-evolutionary risks of not changing seed provenancing practices in changing environments. *Ecology Letters* , e14248.
- Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the earth's land surface areas. *Scientific Data* , **4** , 170122.
- Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2018. Data from: Climatologies at high resolution for the earth's land surface areas. Dryad.
- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecology Letters* , **7** , 1225-1241.
- Lamont, B. B., M. R. Williams, and T. H. He. 2023. Relative growth rate (RGR) and other confounded variables: mathematical problems and biological solutions. *Annals of Botany* , **131** , 555-567.
- Leimu, R., and M. Fischer. 2008. A Meta-Analysis of Local Adaptation in Plants. *Plos One* , **3** , 8.
- Liang, X., Q. Ye, H. Liu, and T. J. Brodribb. 2021. Wood density predicts mortality threshold for diverse trees. *New Phytologist* , **229** , 3053-3057.
- Malavasi, M. D., A. S. Davis, and U. C. Malavasi. 2018. Tree seed sourcing for landscape restoration under climate changes. *Ciencia Florestal* , **28** , 446-455.
- Malcolm, D. T., B. K. A. Nagel, I. Sinclair, and Heiner, I.J. . 1999. Soils and agricultural land suitability of the Atherton Tablelands. In D. o. N. Resources (Ed.).
- Matesanz, S., and J. A. Ramirez-Valiente. 2019. A review and meta-analysis of intraspecific differences in phenotypic plasticity: Implications to forecast plant responses to climate change. *Global Ecology and Biogeography* , **28** , 1682-1694.
- Mcdonald, T., J. Jonson, and K. W. Dixon. 2016. National standards for the practice of ecological restoration in Australia. *Restoration Ecology* , **24** , S6-S32.
- Meek, M. H., E. A. Beever, S. Barbosa, S. W. Fitzpatrick, N. K. Fletcher, C. S. Mittan-Moreau, B. N. Reid, S. C. Campbell-Staton, N. F. Green, and J. J. Hellmann. 2022. Understanding Local Adaptation to Prepare Populations for Climate Change. *Bioscience* , **73** , 36-47.
- Merila, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* , **7** , 1-14.
- Middleby, K. B., A. W. Cheesman, and L. A. Cernusak. 2024a. Impacts of elevated temperature and vapour pressure deficit on leaf gas exchange and plant growth across six tropical rainforest tree species. *New Phytologist* , **243** , 648-661.
- Middleby, K. B., Cheesman, A. W., Hopkinson, R., Baker, L., Ramirez Garavito, S., Breed, M. F. and Cernusak, L. A. 2024b, Ecotypic Variation in Leaf Thermoregulation and Heat Tolerance but Not Thermal Safety Margins in Tropical Trees. *Plant, Cell & Environment* . <https://doi.org/10.1111/pce.15141>
- Mitchard, E. T. A. 2018. The tropical forest carbon cycle and climate change. *Nature* , **559** , 527-534.
- Muehleisen, A. J., B. M. J. Engelbrecht, F. A. Jones, E. Manzano-Pinzon, and L. S. Comita. 2020. Local adaptation to herbivory within tropical tree species along a rainfall gradient. *Ecology* , **101** .
- Muller, K., and D. C. Albach. 2010. Evolutionary Rates in Veronica L. (Plantaginaceae): Disentangling the Influence of Life History and Breeding System. *Journal of Molecular Evolution* , **70** , 44-56.

- Mushagalusa, F. C., D. Bauman, B. M. Bazirake, Y. Mleci, M. Kalenga, M. N. Shutcha, and P. Meerts. 2020. Phenotypic plasticity, not ecotype differentiation, explains the broad ecological niche of a tree species in African dry woodlands. *Environmental and Experimental Botany* ,**178** , 8.
- Offord, C. A., and P. F. Meagher. 2009. Plant germplasm conservation in Australia: strategies and guidelines for developing, managing and utilising ex situ collections. Australian Network for Plant Conservation Inc., Canberra.
- Poorter, L., S. J. Wright, H. Paz, D. D. Ackerly, R. Condit, G. Ibarra-Manriques, K. E. Harms, J. C. Licona, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-Landau, M. Pena-Claros, C. O. Webb, and I. J. Wright. 2008. Are functional traits good predictors of demographic rates?: Evidence from five Neotropical forests. *Ecology* ,**89** , 1908-1920.
- Preece, N. D., M. J. Lawes, A. K. Rossman, T. J. Curran, and P. Van Oosterzee. 2015. Modelling the growth of young rainforest trees for biomass estimates and carbon sequestration accounting. *Forest Ecology and Management* , **351** , 57-66.
- Preece, N. D., P. Van Oosterzee, and M. J. Lawes. 2023. Reforestation success can be enhanced by improving tree planting methods. *Journal of Environmental Management* , **336** .
- Preece, N. D., P. Van Oosterzee, G. C. H. Unda, and M. J. Lawes. 2017. National carbon model not sensitive to species, families and site characteristics in a young tropical reforestation project. *Forest Ecology and Management* , **392** , 115-124.
- R Core Team. 2022. R: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ravn, J., A. R. Taylor, M. B. Lavigne, and L. D'orangeville. 2024. Local adaptation of balsam fir seedlings improves growth resilience to heat stress. *Canadian Journal of Forest Research* , **54** , 331-343.
- Reed, D. H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. *Conservation Biology* , **17** , 230-237.
- Reich, P. B. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* , **102** , 275-301.
- Rejou-Mechain, M., A. Tanguy, C. Piponiot, J. Chave, and B. Hérault. 2017. `<scp>biomass</scp>`: an `<scp>r</scp>` package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution* , **8** , 1163-1167.
- Riahi, K., R. Schaeffer, J. Arango, K. Calvin, C. Guivarch, T. Hasegawa, K. Jiang, E. Kriegler, R. Matthews, G. P. Peters, A. Rao, S. Robertson, A. M. Sebbit, J. Steinberger, M. Tavoni, and V. V. D.P. 2022. Mitigation pathways compatible with long-term goals. In P. R. Shukla, J. Skea, R. Slade, A. Al-Khourdajie, R. van Diemen, D. McCollum, M. Pathak, S. Some, P. Vuyas, R. Fradera, M. Belkacemi, A. Hasija, G. Lisboa, S. Luz and J. Malley (Eds.). In IPCC, 2022: Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge UK, and New York USA.
- Schlaepfer, D. R., B. Braschler, H. P. Rusterholz, and B. Baur. 2018. Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: a meta-analysis. *Ecosphere* , **9** , e02488.
- Schwinning, S., C. J. Lortie, T. C. Esque, and L. A. Defalco. 2022. What common-garden experiments tell us about climate responses in plants. *Journal of Ecology* , **110** , 986-996.
- Smith, M. N., T. C. Taylor, J. Van Haren, R. Rosolem, N. Restrepo-Coupe, J. Adams, J. Wu, R. C. De Oliveira, R. Da Silva, A. C. De Araujo, P. B. De Camargo, T. E. Huxman, and S. R. Saleska. 2020. Empirical evidence for resilience of tropical forest photosynthesis in a warmer world. *Nature Plants* , **6** , 1225-1230.

- Smith, S. A., and J. M. Beaulieu. 2009. Life history influences rates of climatic niche evolution in flowering plants. *Proceedings of the Royal Society B-Biological Sciences* , **276** , 4345-4352.
- Smith, S. A., and M. J. Donoghue. 2008. Rates of molecular evolution are linked to life history in flowering plants. *Science* ,**322** , 86-89.
- Sork, V. L., S. N. Aitken, R. J. Dyer, A. J. Eckert, P. Legendre, and D. B. Neale. 2013. Putting the landscape into the genomics of trees: approaches for understanding local adaptation and population responses to changing climate. *Tree Genetics & Genomes* , **9** , 901-911.
- Stanton, M. L., and D. A. Thiede. 2005. Statistical convenience vs biological insight: consequences of data transformation for the analysis of fitness variation in heterogeneous environments. *New Phytologist* , **166** , 319-338.
- Steane, D. A., B. M. Potts, E. Mclean, S. M. Prober, W. D. Stock, R. E. Vaillancourt, and M. Byrne. 2014. Genome-wide scans detect adaptation to aridity in a widespread forest tree species. *Molecular Ecology* ,**23** , 2500-2513.
- United Nations General Assembly. 2019. Resolution adopted by the General Assembly on 1 March 2019: United Nations Decade on Ecosystem Restoration (2021–2030) A/RES/73/284.
- Vancutsem, C., F. Achard, J.-F. Pekel, G. Vieilledent, S. Carboni, D. Simonetti, J. Gallego, L. E. O. C. Aragao, and R. Nasi. 2021. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances* , **7** , eabe1603.
- Watson, J. E. M., T. Evans, O. Venter, B. Williams, A. Tulloch, C. Stewart, I. Thompson, J. C. Ray, K. Murray, A. Salazar, C. Mcalpine, P. Potapov, J. Walston, J. G. Robinson, M. Painter, D. Wilkie, C. Filardi, W. F. Laurance, R. A. Houghton, S. Maxwell, H. Grantham, C. Samper, S. Wang, L. Laestadius, R. K. Runtz, G. A. Silva-Chavez, J. Ervin, and D. Lindenmayer. 2018. The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution* , **2** , 599-610.
- Willi, Y., and J. Van Buskirk. 2022. A review on trade-offs at the warm and cold ends of geographical distributions. *Philosophical Transactions of the Royal Society B: Biological Sciences* , **377** .
- Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Diaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* ,**91** , 3664-3674.