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RESEARCH ARTICLE

Elevational clines predict genetically determined variation in tropical forest seedling performance in Borneo: implications for seed sourcing to support reforestation

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While much research has focused on genetic variation in plants in relation to abiotic clines in temperate and boreal forests, few studies have examined similar relationships in tropical forests. Genetic variation in desirable performance traits of trees, such as drought tolerance, fast-growth, and carbon sequestration rates, is widely used to improve reforestation efforts in nontropical systems. However, evolutionary processes such as local adaptation are poorly understood in tropical forests making it difficult to locate desired phenotypes. To test for genetic variation in growth rate in relationship to climatic clines, we conducted a common garden study over 18 months in a nursery using four dipterocarp tree species, represented by 9–12 half-sib families, sourced across an elevational gradient ranging from lowland to hill forests (circa 130–470 m above sea-level) in Malaysian Borneo. We found genetic variation in growth for all four species with fast-growing half-sib families growing 42–88% faster than poorly performing half-sib families. Furthermore, in three species we found that elevation of seedling origin predicted seedling performance; in *Shorea fallax* and *S. johorensis*, half-sib families originating from low elevations performed the best. In *S. argentifolia* half-sib families' seedlings from low elevations grew slowly. Because elevation is a good proxy for climate, the finding of elevational clines predicting genetic variation in growth provides evidence of evolution affecting the function of tropical tree species. Our research highlights opportunities to better understand evolutionary processes in tropical forests and to use such information to improve seed source selection in reforestation.

Key words: climate change, Dipterocarpaceae, forest restoration, provenance test, tropical forest evolution, tropical local adaptation

Implications for Practice

- Tree species from the dipterocarp family contain considerable genetic variation in growth that is useful for enhancing restoration or plantation forestry using native tree species.
- Part of this variation in growth rate is predicted by a commonly used proxy of climate variation, that is elevation, a novel result that provides rarely found evidence of local adaptation in tropical forests.
- Increased understanding of evolutionary processes resulting in genetic variation of desirable plant traits could improve seed sourcing guidelines for use in reforestation of tropical forests.

Introduction

Ambitious targets to reforest millions of hectares of degraded tropical forests requires the propagation of seedlings with favorable traits, such as those adapted to future climate scenarios or those that enhance seedling survival, or that are beneficial for maximizing growth and carbon sequestration rates to mitigate climate change (Gregorio et al. 2017). Poorly selected seed sources may result in slow growth and low survival of seedlings and increase the cost of reforestation (Gregorio et al. 2017; Jalonen et al. 2018). Furthermore, with climate change there is

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a need to consider changing biophysical conditions of the future to foresee that restoration is successful (Harris et al. 2006). In cases when locally adapted populations risk becoming maladapted for future climates (Alberto et al. 2013; Isaac-Renton et al. 2018; Barton et al. 2020) there may be a need to ensure that genetic variation can be sustained to promote adaptation or to pre-adapt species used in tropical forest restoration to future climatic conditions (Axelsson et al. 2020). Although such concepts have been well applied in temperate forests due to extensive research into causes of local adaptation, such applications are not yet well-applied to tropical forests where the underlying causes of genetic variation remain poorly understood (Axelsson et al. 2020), but see Barton et al. (2020) and Ng et al. (2021). Predictions of the impacts of climate change to the genetic structure of tropical forests and the consequences to tree performance are untenable without understanding how biotic and abiotic forces shape genetic structure.

Due to the rarity of forest research in the tropics assessing the causes of intraspecific variation of tree species (Grady & Axelsson accepted), we are currently unable to: (1) predict climate change impacts on selection of traits that would be favorable in a future climate, and; (2) predict geographically where we might find traits with desirable properties for use in reforestation. A better understanding of both may have dramatic benefits to the future success of reforestation projects as well as increase the use of native species with desirable properties compared to exotic species that are currently commonly used in tropical reforestation efforts. For example, pioneer Forest Landscape Restoration programs, large-scale projects across thousands of hectares such as those implemented in China (Xu 2011) and South Korea (Temperton et al. 2014), focus almost exclusively on the use of exotic tree species to increase tree cover in deforested landscapes. Because such seedlings are readily available due to their widespread use in commercial forestry, they are cheaper, and easier to obtain than native tree species. Information on native tree seed collection and seedling production is scarce and so they are used less in reforestation and rarely in plantation forestry (Brancalion et al. 2012; Nunes et al. 2016; Moreira da Silva et al. 2017). Improved understanding of the extent and evolutionary causes of functional and adaptive genetic variation of native tree species in tropical forests could be used to direct seed collection campaigns and help improve nursery practices to support reforestation and restoration of native forests. Such information could also help pre-adapt restored native forests to future climates (Axelsson et al. 2020).

Although hyper-diverse tropical forests may contain high genetic variation on small spatial scales (Harata et al. 2012; Tito de Morais et al. 2015; Lee et al. 2016), there is a fundamental lack of information about how this variation may be shaped by broad geographic variation in abiotic factors. Although the distribution of tropical tree species are known to be determined by abiotic conditions such as soil characteristics on small spatial scales (Paoli et al. 2006; Bartholomew et al. 2022) and climate on larger scales (Engelbrecht et al. 2005), whether or not populations are locally adapted to the same abiotic conditions is unclear (Grady & Axelsson accepted). Nevertheless, the importance of such factors has been highlighted in some recent studies (Axelsson et al. 2020; Barton et al. 2020; Ng et al. 2021), for example by Ng et al. (2021) who highlights the evolutionary relevance of drought in aseasonal tropical rainforests. While abiotic variation certainly exists across highly diverse tropical landscapes, how it impacts genetic variation is not well known. Because precipitation is generally high across all rainforests such as in Borneo, and temperatures do not fluctuate greatly, it is possible that precipitation and temperature do not lead to selection. However, while direct adaptation to abiotic conditions such as water availability and temperature may seem unlikely in wet tropical forests, the amount and seasonality of rainfall does vary across elevational gradients. Differences in rainfall are known to alter community composition of trees inferred to be due to adaptive variation that favors some species over others in different environments (Engelbrecht et al. 2005). If this is the case at the inter-specific level, why would it not hold within species at the intra-specific level? Elevation is generally well correlated to environmental and climate variables such as temperature and precipitation and is commonly used to examine how genetic variation may be structured by climate (Grady et al. 2011; Isaac-Renton et al. 2018; Vanhove et al. 2021). Although past research in tropical forests has found genetic variation in plant traits and drought tolerance (Axelsson et al. 2020), such variation has rarely been correlated to abiotic clines such as edaphic, thermal, or precipitation gradients. A better understanding about the influences of abiotic clines on genetic variation in tropical forests could have a tremendous impact on the output of tropical forest restoration such as already shown in other systems (Grady et al. 2015).

Although elevational gradients, by being well-correlated to climate, are known to shape the structure of tree populations, it is difficult to partition the relative strength of the often covarying effects between the biotic and abiotic factors that influence genetic structure. For example, elevational gradients also commonly impact the biotic community that, in turn, may influence selection; that is high elevation tropical forests have lower tree density and overall stand biomass than low elevation forests (Alves et al. 2010; Nasto et al. 2017; Rozendaal et al. 2020). Consequently, the strength of both inter- and intra-specific competition have been shown to vary by elevation in tropical forests (Levine et al. 2016). As a result, competition for light and nutrients may be higher at low elevation, potentially resulting in selection for competitive traits such as fast growth. Additionally, interactions with plant pathogens have been shown to vary by population and climate with plants with certain traits more resistant to pathogens, such that climate change favors certain populations over others in resistance to the combined influences of climate and pathogens (Grady et al. 2015). Nevertheless, although the actual agent of selection may be elusive, assessing if, and in what way, elevational clines shape genetic variation in tree performance would provide a first step into understanding evolutionary processes in action in tropical forests.

We established a common garden experiment in a nursery using four dipterocarp tree species each represented by 9–12 half-sib families collected across an elevational range of 130–470 m above sea-level (a.s.l.) encompassing both lowland dipterocarp forest (<350 m a.s.l.) and hill forests (>350 m a.s.l.). We tested for genetic variation in growth performance in a nursery and assessed to what extent variation was related to differences in elevation among seed sources. We explicitly tested two main hypotheses: (1) genetic variation in growth rate exists among different half sib families, and; (2) this variation is correlated to differences in elevation among seed sources of half sib families suggesting the potential for local adaptation to be influencing the genetic structure of our study species. Elucidating that genetic variation in plant performance corresponds to an elevational gradient is a first step for a better understanding of the evolutionary causes of genetic variation in tropical forests.

Methods

Genetic Material Collection

We established a multi-species common garden experiment in a nursey with four species of dipterocarps (*Shorea argentifolia*, *S. fallax*, *S. johorensis*, and *S. paucifolia*) that are all commonly used in reforestation efforts in mixed-dipterocarp forests of Borneo. All four species have similar habitat requirements and basic characteristics with small differences among species (Table 1). For example, all four species occur on lowland and hill forests but *S. argentifolia* and *S. fallax* are often associated with clay soils while no soil-type association has been reported for *S. pauciflora* or *S. johorensis*. Furthermore, *S. argentifolia* occurs up to an elevation of 700 m a.s.l. while *S. johorensis* typically occurs below 600 m a.s.l. (Table 1). There are information suggesting that tree communities in these forests may be determined by soil variables on small-to-large spatial scales (Russo et al. 2005; Paoli et al. 2006) and climate variables on larger scales (Miyamoto et al. 2021).

We took advantage of a strong mast fruiting year in 2019 to collect seeds from 9 to 12 different mother trees from each of four species. All seeds were collected between August 19 and September 11, 2019. All seed collections were done within an area framed by Imbak Canyon conservation area in the north, Danum Valley INFAPRO Rainforest rehabilitation project to the east, INIKEA-Sow-a-seed restoration project to the south, and Maliau Basin conservation area to the west (Fig. 1). We designed the collection to be as logistically efficient as possible and most collection was done in areas accessible by roads. We made sure to cover an elevational gradient ranging from approximately 130 m a.s.l. to approximately 470 m a.s.l. as recorded with a GPS-devise (Table 2) but due to difficulty in finding the same trees at all collection sites, the distribution of mother trees across the gradient varied among the different species. We used elevation as a proxy for a combination of covarying abiotic factors such as precipitation and temperature because they are well correlated and together often influence variation among traits of different plant populations. Due to the physical remoteness of our population seed sources, reliable weather data were not available for our source populations. Nevertheless, our rough estimates based on data from four weather stations covering the full range of elevations of our seed collections (i.e. Tawau airport at 17 m a.s.l., Luasong at 300 m a.s.l., Danum valley at 427 m a.s.l., and Maliau basin at 500 m a.s.l.) suggests that these populations would experience an average precipitation of 155 mm/month in low elevation populations and 262 mm/month in high elevation populations, representing an increase of approximately 60% from low to high elevations (Fig. 2). Such a difference has been shown to influence vegetation dynamics (Engelbrecht et al. 2005), and here, we examine if this same degree of variation might impact evolutionary dynamics. The climatic differences across our gradient of collection are also reflected in air temperature with higher temperatures at lower elevations. For example, at the airport in Tawau, the mean daily maximum air temperature is 1.4°C higher than at Maliau Basin (30.1 vs. 28.7°C). This gradient also covers both lowland mixed-dipterocarp forest (<350 m a.s.l.) and hill forests (>350 m a.s.l.) that differ in tree species composition and forest structure (Manokaran & Kochummen 1994). For example, dipterocarp hill forests are dominated by slow growing species whereas faster growing species are more commonly found in lowland mixed-dipterocarp forests of southeast Asia (Manokaran & Kochummen 1994). All seeds were collected from the forest floor underneath individual mother trees separated from each other by at least 100 m to ensure that collected materials were distinct half-sib families (i.e. maternal lines). Seeds were germinated on seedbeds in the INIKEA nursery in Luasong (4°37.43′N, 117°12.15′ E, a.s.l. 300 m) immediately following collection.

After germination, seeds were planted in polyethylene bags (6 cm diameter by 40 cm height) filled with soil as a mixture of mineral soil and compost at a ratio of 1:1. The compost was

Table 1. Basic ecological and physiological characteristics of four dipterocarp tree species used to test for elevational clines in a nursery-based common garden experiment in Sabah, Malaysia on the island of Borneo. *Source*: Data compiled from Ghazoul (2016).

Tree species	*Occurrence*	*Elevation*	*Wood density*
Shorea johorensis	Locally common and occur on well-drained flat and undulating land	Below 600 m	320–695 kg/m^3
S. argentifolia	Locally abundant and gregarious and is found on clay soils, usually on undulating land and valleys	Up to 680 m	480–835 kg/m^3
S. pauciflora	Occur on well-drained deep soils in lowland and hill forests up to 700 m altitude	Up to 700 m	490–835 kg/m^3
S. fallax	Locally frequent on clay soils in mixed dipterocarp forests on well drained flat or hilly sides	Up to 600 m	560–960 kg/m^3

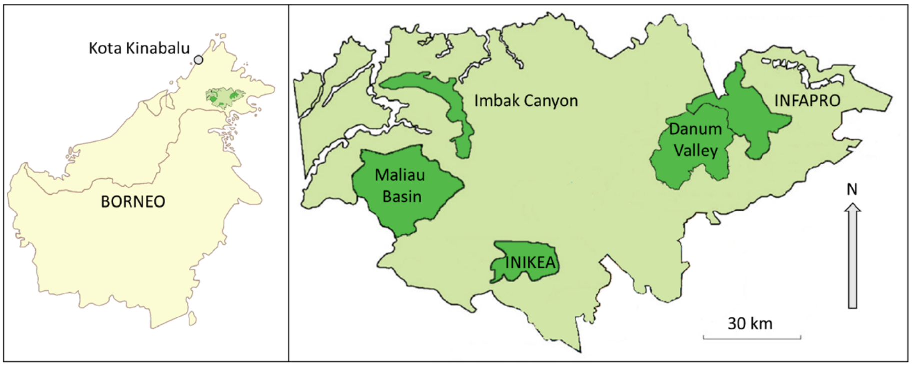

Figure 1. Map highlighting the location of Yayasan Sabah's management concession in Sabah, Borneo, Malaysia in green, with the area of seed collection for assessing geographically determined genetic variation in seedling growth roughly framed by Imbak Canyon conservation area in the north, INFAPRO Rainforest rehabilitation project to the east, INIKEA-Sow-a-seed restoration project to the south, and Maliau Basin conservation area to the west.

produced by mixing saw dust, dry grass, and urea into locally collected mineral soil, and kept for approximately 6 months prior to using for potting. To account for environmental variation within the nursery, we distributed all half-siblings into five distinct areas within the nursery (blocks) and within these blocks we ensured that each half-sib family was represented by at least one seedling (range: 1–6, median: 2) in each of seven sub-blocks. This was done to ensure that all species and half-sibs were exposed to the same range of environmental conditions within the nursery. The shade house included mesh screen approximately 2.5 m height as a ceiling and was open to the air around the perimeter. In February 2021, we recorded the height as measured from the soil surface to the top of the highest green leader of each plant and diameter at root collar (2 cm above soil surface) of all seedlings. These measurements correspond to the size gained since collection of un-germinated seeds and represents a measure of nursery growth performance which is crucial for effective propagation of viable seedlings for out-planting. The time elapsed from seed collection to the seedling size measurement varied between 523 and 546 days. The variation in time between collection and measurements among half-sib families was 2.8% for *S. johorensis*, 3.5% for *S. argentifolia*, 3.7% for *S. fallax*, and 4.2% for *S. paucifora*.

Statistical Analyses

We used general linear models to test for genetic effects on nursery growth performance (seedling height and seedling collar basal area). To account for slight differences in seed collection dates, we normalized seedling height and collar diameter by the number of days elapsed between seed collection and measurements in the nursery. As the data were normally distributed, we ran analyses on untransformed data using a normal distribution model. To account for possible environmental variation within the nursery, we used the five growing areas in the nursery as a random blocking factor in all analyses. As the seven sub-blocks within each main block sometimes included more than one seedling per full-sib family, we used mean values for each of the seven sub-blocks in our analyses to ensure independence.

Table 2. Number of half-sib families of four tree species of the dipterocarp family used in a nursery-based growth performance common garden experiment in the town of Luasong in Sabah, Malaysia on the island of Borneo. The different half-sib families originate from a geographical gradient that varies in elevation from roughly 128 to 476 m a.s.l. depending on species.

Species	*Half-sib families*	*Elevation range*
Shorea argentifolia	12	129–476
S. fallax	12	129–464
S. johorensis	9	129–423
S. pauciflora	11	128–417

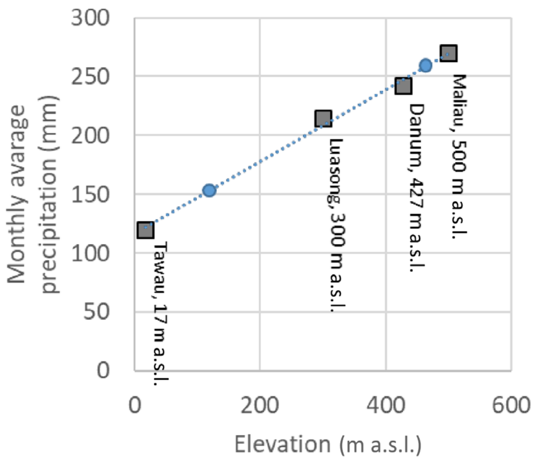

Figure 2. Patterns of monthly average precipitation (mm) across an elevational gradient ranging across Tawau airport at 17 m a.s.l., Luasong at 300 m a.s.l., Danum valley at 427 m a.s.l., and Maliau basin at 500 m a.s.l. Blue dots represent elevational ranges (maximum and minimum) of half-sib seed collection. Across the range of seed collection sites, populations are expected to face an increase in precipitation from 155 to 262 mm (~60%). Tawau data are from a meteorological station at the Tawau airport and was compiled from https://www.meteoblue.com/ between 1992 and 2022. Data for Luasong is from records from the INIKEA restoration project northwest of the town of Luasong and represents the period of 2004–2016. Data for Danum and Maliau was compiled from the Danum Valley Research Station and Maliau Basin Research Station weather stations between 2010 and 2016.

With five blocks and seven independent samples in each block our sample size was 35 per half-sib family. For the species that showed genetic variation in growth performance, we also tested to what extent growth performance varied by elevation (as it happened, all four species revealed a significant effect of half sib family and hence all four species were included in the second analysis). To accomplish this, we ran linear regressions between mean seedling performance of each half-sib family and elevation of the seed source (that is, mother tree). All statistical analyses were conducted in JMP16 pro (SAS 2020–2021). We tested for significance at the 0.05 alpha level.

Results

Our first hypothesis that different half sib families varied in nursery growth rate was supported for all four species and for both height and diameter ($p < 0.005$ in all cases; Table 3). Normalized growth rate of top performing half-sibs was 32–74% (height) and 42–88% (basal area) higher than growth of the most poorly performing half-sibs depending on species (Table 4).

Confirming our second hypothesis that part of this variation was related to the elevation of the seed source of the seedlings, we found a significant correlation between performance and elevation for three out of our four study species (Fig. 3). In *Shorea argentifolia* half-sib families' originating from an elevation of 476 m grew roughly 55% larger in basal area than families originating from an elevation of 130 m. In *S. fallax* and *S. johorensis*, half-sib families originating from low elevations performed the best. In *S. fallax*, families originating from an elevation of 130 m grew approximately 40% more in basal area compared to families originating from an elevation of 460 m. The *S. johorensis* families originating from an elevation of 130 m grew 25% more in diameter than families originating from 420 m elevation. Taken together, these results suggest that elevation as a proxy for climate, resulted in natural selection for three out of four species in a tropical forest.

Discussion

In tropical forests, current limited understanding of whether or not, and to what degree, genetic variation is related to environmental gradients, such as temperature or precipitation clines, limits our ability to: (1) fully understand evolutionary processes and the mechanisms underlying genetic structure in tropical forests; (2) predict population response to climate change, and; (3) predict where to locate plant material with desirable traits linked to growth, carbon sequestration rate, and drought tolerance; all factors that may improve reforestation success to restore degraded landscapes and mediate climate change. We found considerable genetic variation in growth performance in all four species tested and that growth rate by top performing half-sib families was up to 88% higher than the growth rate of the most poorly performing half sib families. In three out of four species, we also found that part of this variation could be predicted by elevation and likely reflects local adaptation to climate. Our research demonstrates the potential for incorporating naturally occurring genetic variation into reforestation efforts to enhance performance of seedlings in all of the study species examined (four out of four species). Our results also indicate that we can locate desirable growth characteristics based on the elevation of seed collection sites (three out of four species) but that seed sourcing guidelines will vary by species because the relationship between seedling performance and elevation varies by species. We used elevation as a proxy for a combination of covarying abiotic factors such as precipitation and temperature because it has often been found to be well correlated to variation among traits of different plant populations, and

Table 3. Results from generalized linear models testing for the effect of half-sib family and block on seedling performance, that is height and diameter gained in the nursery of four different species of dipterocarps growing for 18 months. Bold *p*-values denote statistical significance at $p < 0.05$.

		Basal area			*Height*		
	DF	*SS*	F	p	*SS*	F	p
Shorea argentifolia							
Half sib family	11	0.038	13.019	**<0.0001**	0.050	10.961	**<0.0001**
Block	4	0.004	3.723	**0.006**	0.006	3.410	**0.010**
Half sib family × block	44	0.007	0.647	0.960	0.013	0.700	0.925
S. fallax							
Half sib family	11	0.054	15.361	**<0.0001**	0.050	12.191	**<0.0001**
Block	4	0.001	0.686	0.602	0.003	2.161	0.073
Half sib family × block	44	0.016	1.101	0.314	0.012	0.733	0.895
S. johorensis							
Half sib family	8	0.012	4.581	**<0.0001**	0.024	4.788	**<0.0001**
Block	4	0.000	0.340	0.851	0.003	1.275	0.281
Half sib family × block	32	0.015	1.457	0.062	0.013	0.639	0.935
S. pauciflora							
Source							
Half sib family	10	0.006	2.624	**0.005**	0.032	7.435	**<0.0001**
Block	4	0.002	2.047	0.088	0.010	5.633	**<0.001**
Half sib family × block	40	0.006	0.646	0.952	0.010	0.557	0.9863

Table 4. Genetic variation among half-sib families of four different tree species in seedling performance in the nursery with percentages relating to relative differences of top performing half-sib families in comparison to poorly performing half-sib families. "Realized" refers to the actual size gained in the nursery and "Normalized" refers to the size adjusted for slight differences in seed collection dates.

	Height		*Basal area*	
Species	*Realized*	*Normalized*	*Realized*	*Normalized*
Shorea argentifolia	41%	39%	85%	88%
Shorea fallax	74%	72%	78%	80%
Shorea johorensis	30%	32%	61%	60%
Shorea pauciflora	75%	74%	41%	42%

because weather station data were not available for the physical location of our seed sources. Although we are not able to pinpoint the exact agent of natural selection, predictable phenotypic variation across an elevational cline is evidence of local adaptation, and surprisingly, one of the first evidences of local adaptation in a tropical forest.

Partitioning between abiotic and biotic drivers resulting in local adaptation is not possible in our current study, but we speculate why both abiotic and biotic components may be involved in local adaptation processes. Mixed-dipterocarp lowland forests (low elevation) and mixed-dipterocarp hill forests (high elevation) vary considerably in biotic and abiotic conditions that may both impose a suite of selection pressures to natural populations (Barton et al. 2020). For example, although soil water availability to plants is high in wet tropical forests our rough estimates suggest that families sourced from high elevation hill forests experience roughly 60% more precipitation than those from lowland forests. As a consequence, reoccurring El Niño droughts are expected to be more severe in lowland forests compared to hill forests (Miyamoto et al. 2021). Such droughts may then influence genetic structure resulting in phenotypic variation in drought tolerance (Axelsson et al. 2020, 2021; Ng et al. 2021). Variation in precipitation has commonly been found to structure populations in other nontropical systems (Alberto et al. 2013; Postolache et al. 2021). Although scarce evidence of similar patterns of local adaptation exists in tropical forests, one such case has been illustrated in Hawaii where Barton et al. (2020) found that populations exposed to low versus high levels of precipitation were more drought tolerant in the widespread tropical tree, *Metrosideros polymorpha*. However, covarying with precipitation is lower temperature, lower soil nutrient availability from higher leaching rates, reduced plant competition, and potential variation in herbivore and pathogen loads, all with high potential to influence the causes of local adaptation. It is beyond the scope of our paper to partition the potential for these different factors and their interactions to

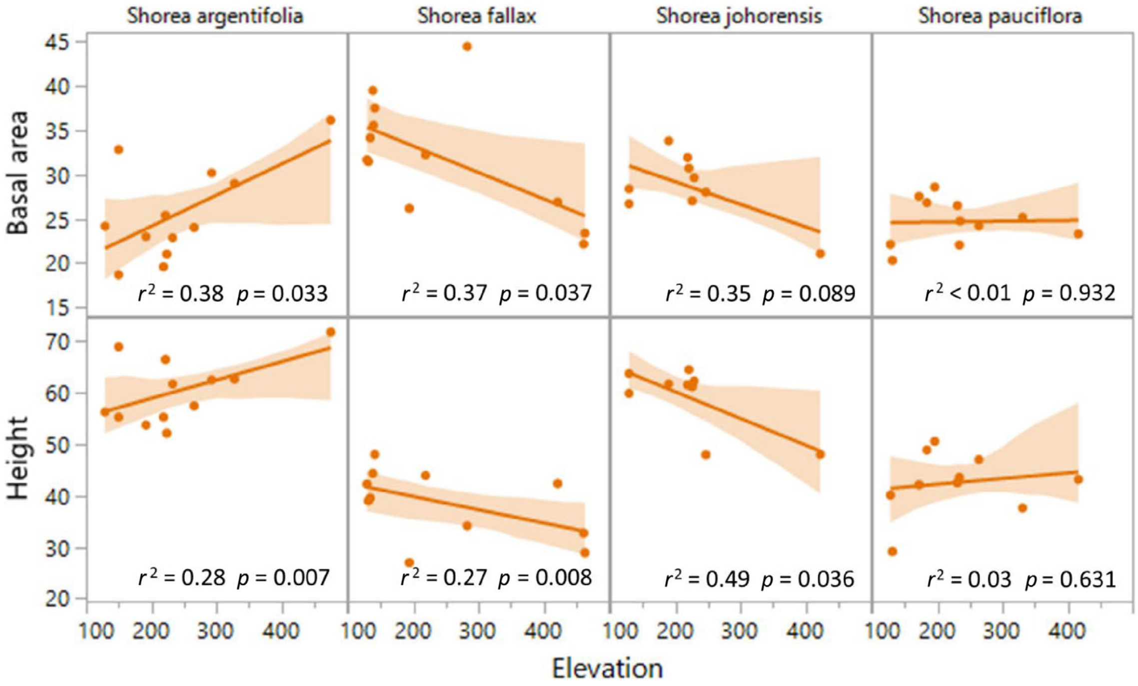

Figure 3. Relationship between growth performance, height (cm), and basal area (mm^2) of half-sib families of four different species of seedlings in the nursery and the elevation of the locality of the mother tree origin. Shaded areas refer to 95% CI.

influence local adaptation and certainly much research is needed to disentangle these factors. While we are unable to tease apart the evolutionary mechanisms responsible for genetic divergence, it is still worth highlighting that elevational gradients can help us locate different and desirable phenotypes. Whether or not we understand how they evolved, we can still start to test their use in reforestation trials to achieve restoration objectives. We could pre-adapt forests to climate change such as through increasing the frequency of drought-tolerant phenotypes on the landscape or use a wider range of genetic material as a bet-hedging approach to cope with environmental uncertainty (sensu Axelsson et al. 2022).

In addition to the difficulty in identifying the underlying mechanisms of local adaptation, that is, the specific or multiple selection agents, our research also suggests the compounded complexity that such selection agents may differ among species. We found that the effect of elevational clines on genetic variation in seedling growth was idiosyncratic among species suggesting that selection agents may differ among species. In two species, families from lower elevations had higher growth than those from higher elevations, whereas we found the opposite in one species, and no pattern in a fourth species. Clearly, environmental variation can impose diverging selection pressures across climate gradients (Alberto et al. 2013; Kremer et al. 2014) and the direction of selection may depend on species specific constraints making some strategies viable for some species but not others (Vitasse et al. 2009; Alberto et al. 2013). Vitasse et al. (2009) demonstrated that genetic-based elevational clines resulted in phenotypic variation taking different directions depending on tree species. In another study, using three species growing in a common garden in a temperate riparian environment, phenotypic variation among populations differed by species with some species showing a high degree of variation and others none (Grady et al. 2011). These variable results among species are not surprising given the complexity of species strategies for coping with and adapting to dynamic and interactive evolutionary forces.

The production of native seedlings with optimal traits for desired functionality is a significant bottleneck for achieving ambitious global reforestation goals (Gregorio et al. 2017). Our results suggest that nursery-based screening approaches can be used to identify genetic variation in desirable traits or functions such as seedling growth performance, drought tolerance (Axelsson et al. 2020), and even to support the rebuilding of tree-associated canopy arthropod diversity via traits that correlate to foundation genotypes (Axelsson et al. 2022). Our finding of genetic variation in growth performance in the nursery of up to 88% within species reveals a high potential to use standing genetic variation of tropical tree species to speed up production by shortening the time from seed collection to out-planting. As seedling size is a strong predictor of survival of planted seedlings (Andivia et al. 2021; Banin et al. 2023) it could also be possible to utilize standing genetic variation to produce more vigorous seedling that may have a better chance to survive after out planting. Faster growing seedlings may also have higher potential to better compete with weedy vegetation at restoration sites. However, we acknowledge that although fast growth may be beneficial in some environments such as aseasonal forests in southeast Asia, other traits may be important in more stressful environments or during climate change. For example, allocation of resources to roots may also be important for performance of out-planted seedlings during droughts, which highlights a need to explore such relationships in future studies. Furthermore, it is possible that other mechanisms such as plasticity may help seedlings cope with environmental stress (Cooper et al. 2019; Bartholomew et al. 2022; Eisenring et al. 2022) but it is unclear how plasticity may vary within and among species. Despite such caveats, our demonstration of considerable genetically determined variation in growth performance related to elevational clines opens up a novel line of inquiry into a field that is poorly studied in tropical forests. By knowing where to find fast-growing genotypes, that is, at high or low elevation forest stands, and exploring genetic correlations among relevant traits, there is high potential to increase the ability to identify desirable phenotypes for reforestation.

Our research also highlights the potential for incorporating genetic variation of native tropical tree species for production forestry purposes. The goals of forest and landscape restoration include restoring degraded landscapes to provide social, ecological, and economic benefits to local communities (Sabogal et al. 2015). In large parts of the tropics, exotic tree species are often preferred over natives in plantation forestry due to their high productivity potential (Piotto et al. 2004). Similarly, pioneer Forest landscape restoration (FLR) programs, have relied heavily on the use of exotic tree species (Xu 2011; Temperton et al. 2014). The potential for harnessing genetic variation of native tree species has been demonstrated in nontropical systems to enhance growth in forestry timber production systems (Savva et al. 2008; Wang et al. 2010) and in the design of assisted migration approaches to maintain production with climate change (Grady et al. 2015; Zucchi et al. 2017; Dixit et al. 2021). This has previously not been possible in tropical forests due to the overall lack of studies evaluating intra-specific variation in traits and local adaptation. We are aware of very few studies assessing genetic variation using common garden approaches in the tropics (Ramirez-Valiente & Cavender-Bares 2017; Axelsson et al. 2020) and a strategic use of genetic resources is not currently being widely applied to reforestation efforts in the tropics (Thomas et al. 2014). Although we recognize that growth rates in our short duration study in the nursery may not translate directly to growth rates in larger harvestable trees, our results do provide evidence of genetic variation in growth that should be further explored for increasing incentives to incorporate native trees into FLR and plantation forestry. Furthermore, seedling size is a strong predictor of seedling performance (Andivia et al. 2021; Banin et al. 2023) which would imply that our findings in the nursery could be translated to performance in the field.

Although our study highlights the potential to use genetic variation for enhancing outcomes of reforestation and restoration of native tropical forests, future studies will need to assess how genetic variation can be utilized in field operations. Our study was conducted in the nursery at one site and may tell us little about performance in large-scale reforestation operations across landscapes that may vary in environmental conditions. Our study highlights, however, that climatically determined variation is likely imposing selection in these systems, a finding that has clear consequences for reforestation. More research is evidently needed to assess how local adaptation may influence site matching and how such site matching may change as a consequence of climate change. Our study illustrates that evolutionary information on the influence of climate on genetic variation has high potential to enhance outcomes of reforestation and forest restoration. Our research highlights opportunities to better understand evolutionary processes in tropical forests and to use such information to improve seed source selection in reforestation efforts. We propose that multi-species common garden experiments, preferably planted across multiple sites in combination with genome-wide association studies would be suitable for building a better understanding of evolutionary processes in tropical forests.

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