Trait-environment interactions influence tree planting success in Peruvian tropical dry forests

Running title Trait-environment interactions influence restoration success

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WG, SM, BM conceived and designed the research; WG, JCSQ carried out the fieldwork; WG, SM, KVM analysed the data; WG drafted the manuscript; TF, BM, JCSQ, KVM, SM critically reviewed the manuscript

Keywords

- Forest restoration
- Resource-use strategy
- Seedling growth and survival
- Trait-environment interactions
- Tropical dry forests

Abstract

Tropical dry forests are among the most endangered ecosystems globally, despite their critical socio-ecological importance. In recent decades, various tree-planting initiatives have been undertaken to restore these forests, yielding mixed results. To enhance restoration effectiveness, it is imperative to adopt a predictive approach, focussing on the drivers of seedling performance and their interactions. This study explores how tree species traits and environmental conditions interact to influence survival and growth rates in the Tumbes-Piura tropical dry forests of northwestern Peru. Our findings support the widely accepted *growth-mortality* hypothesis, indicating that acquisitive species characterised by a high specific leaf area and low wood density achieve faster growth but experience higher mortality compared to conservative species. According to the general resource-use theory, these acquisitive species are also more sensitive to variations in water and nutrient availability, showing steep declines in growth and survival rates as site conditions become less favourable. Interestingly, we found that the *growth-mortality* hypothesis holds along environmental gradients, with acquisitive species maintaining their high growth rates even under resource-poor conditions, but at the cost of greater vulnerability to mortality. In contrast, the growth rates of conservative species increase markedly when water and nutrients become less limiting. These insights underscore the importance of considering trait-environment interactions in planning tree-planting projects and adapting the management strategy to overall restoration objectives. By doing so, we can improve the outcomes and sustainability of restoration efforts in tropical dry forests.

Implications for practice

- The *growth-mortality* hypothesis holds along resource gradients in tropical dry forest restoration.
- Acquisitive species can exhibit high growth rates even in resource-poor sites, which comes at the cost of higher mortality. Increasing successful establishment through irrigation and fertilization will likely accelerate forest recovery in these restoration sites.
- Planting conservative species in less favourable sites is a more viable option when economic resources are limited, offering a more certain, albeit slower, forest establishment without the need for intensive management.
- Our findings highlight the importance of accounting for trait-environment interactions when evaluating restoration success in future studies.

INTRODUCTION

All around the globe, forests face significant threats from deforestation and degradation, leading to biodiversity loss, accelerating climate change and casting negative impacts on human well-being (HLPE 2017; FAO & UNEP 2020). In response to these alarming trends, there has been a surge in ambitious commitments to restore degraded forest ecosystems across all continents (Sewell et al. 2020). This restoration movement is further amplified by the current 'UN Decade on Ecosystem Restoration' (2021-2030), which underscores the urgency to revive damaged ecosystems (United Nations General Assembly 2019).

Many restoration initiatives involve the active planting of trees to speed up ecosystem recovery (Brancalion & Holl 2020; Lamb et al. 2005), which is particularly important in tropical dry forests (TDFs) that experience a dry season of several months (Mooney et al. 1995). Active planting can considerably accelerate forest establishment in these areas, where natural recovery is often slow and uncertain due to the highly fragmented state of the forests and harsh microclimatic conditions (Alvarez-Aquino & Williams-Linera 2012; Dimson & Gillespie 2020; Griscom & Ashton 2011).

Despite their global socio-ecological importance in housing numerous endemic species and supporting the livelihoods of some of the world's poorest communities (Blackie et al. 2014; Schröder et al. 2021; Banda et al. 2016), TDFs remain among the most threatened terrestrial ecosystems (Miles et al. 2006; Janzen 1988; Hoekstra et al. 2005). The urgency to restore these key systems has led to various TDF restoration initiatives (Campo et al. 2023; Dimson & Gillespie 2020; Cárdenas et al. 2022). However, tree planting as a means of TDF restoration often yields variable and disappointing outcomes in terms of growth and survival rates (Dimson & Gillespie 2020; Werden et al. 2023), despite substantial investments of resources (Birch et al. 2010; Griscom & Ashton 2011). Restoration ecology is therefore urged to become more predictive by studying the factors influencing seedling performance regarding growth and survival (Campo et al. 2023; Brudvig & Catano 2021; Lanuza et al. 2020). Both the identity of the planted species and the environmental conditions at the planting site play a crucial role in governing growth and survival rates (Rosell et al. 2022; Werden et al. 2020). Hence, understanding how these factors relate to each other is key to successfully adapting restoration designs to site-specific contexts and improving overall restoration success (Eviner

& Hawkes 2008; Zirbel & Brudvig 2020; Werden et al. 2023).

The functioning of species can be summarised by placing them along the *acquisitive-conservative* functional trait spectrum (Díaz et al. 2004; Wright et al. 2010). By grouping species with similar resource-use strategies, we can identify and predict their response to environmental gradients (Pinho et al. 2019) and adapt management practices accordingly (Eviner & Hawkes 2008). In TDFs, interactions between traits and environmental conditions have already been used to study differences in the functionality of species assemblages along various edaphic, climatic and topographic gradients (Méndez-Toribio et al. 2017; Comita & Engelbrecht 2009; Pinho et al. 2019). Given that the composition of these assemblages depends strongly on seedling performance (Pinho et al. 2019; Sterck et al. 2011), the observed importance of trait-environment interactions indicates their significance for tree growth and survival.

TDF species have developed distinct resource-use strategies to cope with the seasonally limited water availability, which is widely regarded as the main limiting factor for seedling growth and survival in these forests (Alvarez-Aquino & Williams-Linera 2012; Méndez-Toribio et al. 2020; Markesteijn & Poorter 2009). On the one hand, drought-avoidant acquisitive species are usually deciduous and characterised by a rapid growth response to changes in water availability (Rosell et al. 2022). They possess relatively large transpirational tissues (i.e. high specific leaf area (SLA)) and low wood density (WD), which enable high hydraulic conductivity during the wet season and considerable water storage capacity to bridge short dry periods (Poorter et al. 2019; Sterck et al. 2011; Matlaga et al. 2024). In contrast, drought-tolerant conservative species, with higher wood density and lower SLA, prioritise protecting their retrieved resources, resulting in lower growth rates but enhanced stress tolerance and survival (Werden et al. 2018).

General resource-use theory predicts that acquisitive species perform better under resource-rich, favourable conditions, but that their performance decreases rapidly when resources become scarce (Méndez-Toribio et al. 2020; Worthy et al. 2020; Mira et al. 2023). Indeed, the high growth rate of acquisitive species drops rapidly when water (Sterck et al. 2011) or soil nutrient levels (Baribault et al. 2012; Reich 2014) become limiting. Low soil water availability or high evaporative demand increases the water potential difference between soil and

atmosphere (Bauman et al. 2022; Méndez-Toribio et al. 2020), causing acquisitive species to close their stomata to prevent hydraulic failure, resulting in lower growth rates and potentially even carbon-starvation-induced mortality after prolonged drought (McDowell et al. 2008). Conservative species are less sensitive to hydraulic failures and can maintain photosynthetic activity under drier conditions (Sterck et al. 2011; Matlaga et al. 2024). Similarly, acquisitive species require higher soil fertility, giving them a growth advantage in fertile soils but posing challenges when soil nutrients become limiting (Worthy et al. 2020; Reich 2014). Moreover, it has been suggested that acquisitive species are more sensitive to higher temperatures than conservative species (Sastry & Barua 2017), although this was not confirmed by Slot and Winter (2017). An additional important characteristic of species in TDFs is the ability to fix atmospheric nitrogen, which gives nitrogen-fixing species a competitive advantage over non-fixing species through increased photosynthetic activity and water-use efficiency (Pellegrini et al. 2016; Menge & Chazdon 2016).

In summary, seedling performance is influenced by both species identity and site-specific environmental context, and their interactions might play a pivotal role in restoration practices (Caleño-Ruiz et al. 2023; Zirbel & Brudvig 2020; Mira et al. 2023). These interactions potentially explain some of the observed variability in restoration outcomes (Dimson & Gillespie 2020). Most research on drivers of tree performance and their interactions has focussed on tropical rainforests (e.g. Matlaga et al. 2024; Worthy et al. 2020), often neglecting the TDF biome (Campo et al. 2023; Schröder et al. 2021). With this study, we aim to improve our understanding of how functional traits and environmental factors interact to influence seedling performance in TDF restoration projects. We focus on the Tumbes-Piura dry forest region of northwestern Peru, thereby contributing to improved tree-planting practices in the area (Cerrón et al. 2019; Fremout et al. 2022).

Specifically, we evaluate the impacts of interactions between abiotic (i.e. climate and soil) conditions and adult functional traits (i.e. WD and SLA) of ten tree species on the performance (i.e. growth and survival) of planted seedlings across nine restoration sites over a gradient of environmental conditions. We expect acquisitive species (with low WD and high SLA) to (1) thrive in fertile sites with low atmospheric aridity, showing relatively low mortality and higher growth rates, but (2) be more sensitive to low resource availability compared to conservative species (Sterck et al. 2011; Zirbel & Brudvig 2020). In other words, we anticipate little variation

in growth and mortality rates of conservative species across the studied environmental gradient, while acquisitive species are expected to show relatively high mortality and low growth rates in unfavourable conditions, but better performance as site conditions improve (Matlaga et al. 2024).

MATERIALS AND METHODS

Study sites and region

To evaluate the drivers of tree planting performance, we visited nine restoration sites in the lowland Tumbes-Piura dry forests in northwestern Peru (Figure 1), situated between the Pacific coast and the Andean mountain range up to altitudes of 500 m.a.s.l. (Linares-Palomino 2006). Average annual precipitation in the Tumbes-Piura region varies between 100 and 500 mm, of which around 85% is centred between January and April (Best & Kessler 1995; Cueva-Ortiz et al. 2020). Temperature exhibits a comparable seasonal pattern, with mean annual values varying between 20 and 26°C (Cueva-Ortiz et al. 2020). Every 3 to 7 years, the El Niño Southern Oscillation (ENSO) brings more intense rains to the region, with precipitation levels up to ten times higher than the climatic mean, fostering higher tree recruitment and growth rates (Best & Kessler 1995).

The Tumbes-Piura dry forests are part of the Tumbes-Chocó-Magdalena biodiversity hotspot (CEPF 2005) and are renowned for their endemism (Best & Kessler 1995; Linares-Palomino et al. 2010). Nonetheless, substantial portions of these forests have been lost through deforestation (Escribano-Avila et al. 2017), and much of the remaining patches are strongly degraded due to overgrazing by livestock and – often illegal – logging (Fremout et al. 2020; Linares-Palomino 2006). In recent years, the region has witnessed many restoration efforts to reverse this trend, aiming to restore forest cover and structure, conserve biodiversity, and raise awareness among the local population (Cerrón et al. 2019). Between August and September 2022, we visited nine tree-planting restoration sites in the area that varied in size (0.22 - 12.7 ha), planting year (1988 – 2022), and species composition (Supplement S1). Three suitable sites were obtained from the project database of Cerrón et al. (2019) and complemented with six restoration projects suggested by three restoration managers active in the region. The sites covered a gradient in climatic conditions such as potential

evapotranspiration (1603 - 1968 mm/year), mean annual precipitation (63 – 188 mm) and mean temperature of the wettest quarter (22.75 – 27.05 °C).

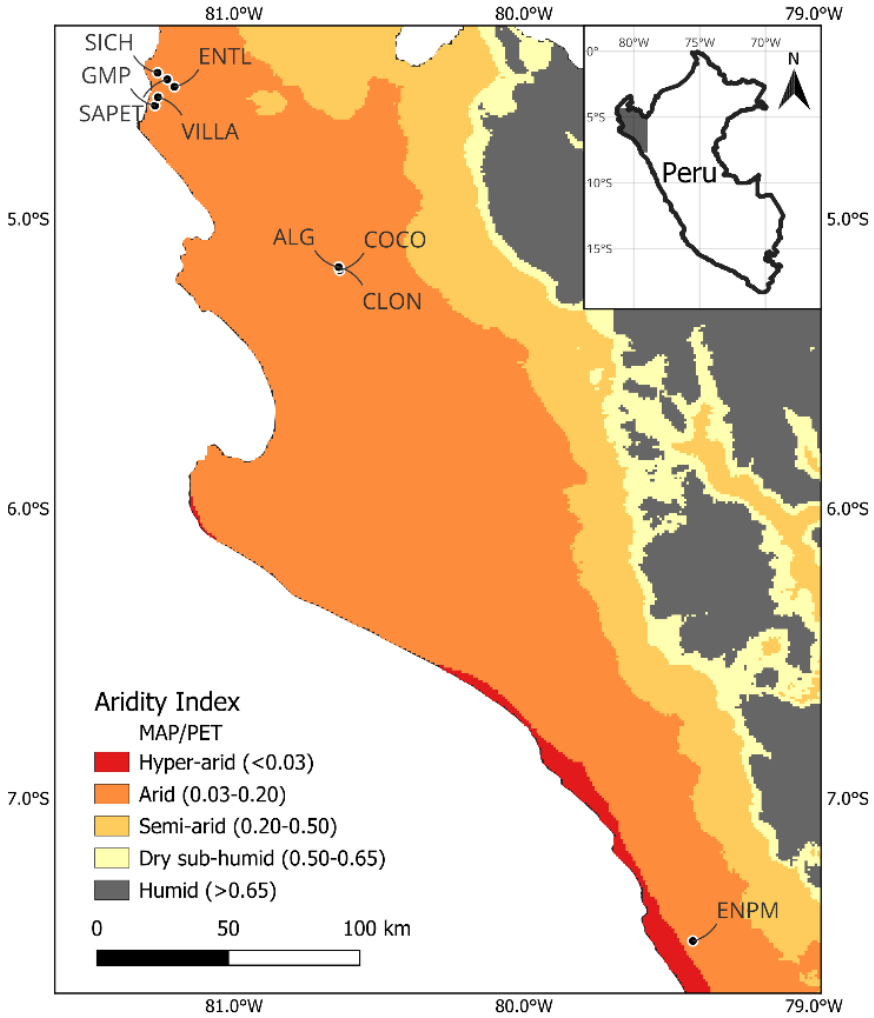

Figure 1: Aridity index map (mean annual precipitation divided by potential evapotranspiration (MAP/PET) following Zomer et al. (2022)) and site locations in the study area in northwestern Peru. Map generated using QGIS 3.34.0 (QGIS Development Team 2024).

Abiotic conditions

Both climate and soil conditions were incorporated to assess the importance of environmental conditions for planted seedling performance (Supplement S1). We extracted climate variables for every site from the CHELSA 2.1 Climate Database (Karger et al. 2017) for the period 1981 to 2010 in QGIS 3.34.0 (QGIS Development Team 2024). These variables, with a resolution of 30 arcsec (ca. 0.9 km at the equator), included mean annual temperature (MAT), mean daily

air temperatures of the wettest (BIO8) and driest (BIO9) quarter, mean annual precipitation (MAP) and mean annual potential evapotranspiration (PET), computed by summing up monthly averages. To account for soil variability, eight subsamples were collected at each site and combined using the quartering method (EPA 2023) to produce one representative composite sample (Pennock et al. 2006). The subsamples were taken at depths of 10, 20 and 30 cm from eight separate locations arranged in a zigzag pattern to ensure even distribution. For two sites exhibiting clear soil heterogeneity, multiple composite samples were acquired from different zones to assess within-site variance, resulting in four composite samples (i.e. 4 × 8 subsamples) at site ENTL and two at site SAPET. The composite soil samples were then air-dried and stored in plastic bags until analysis at the *Universidad Nacional Agraria La Molina* for key factors important for soil fertility (Supplement S1).

Functional traits

To evaluate the effect of functional traits on seedling performance, we included WD, SLA and nitrogen fixation as explanatory variables (Supplement S2). WD [g/cm³] and SLA [cm²/g] were measured for five species (i.e. *Neltuma pallida, Beautempsia avicenniifolia, Parkinsonia aculeata, Lycium boerhaviifolium* and *Morisonia scabrida*), while for *Loxopterygium huasango* only SLA was obtained in the field. For the SLA and WD values of other species, we used literature data as we could not identify suitable candidates to sample in the field. Similarly, the ability to fix atmospheric nitrogen was obtained from literature for all studied species.

SLA was determined by collecting ten undamaged leaves fully exposed to the sun from two to four isolated mature individuals near the restoration sites (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). We included the leaf petioles and did not subdivide compound leaves into individual leaflets. Fresh leaf area was calculated in the software program ImageJ (Schneider et al. 2012) following the protocol of O'Neal et al. (2002). After oven-drying the leaves for 48 hours at 80 °C and measuring their mass, the SLA was calculated by dividing the leaf area by the oven-dry weight. For the wood density measurements, we sampled mature individuals in the vicinity of the planting sites with a tree increment borer (Chave 2006). The extracted cores were stored in paper straws, dried at 80°C for 48 hours (Cornelissen et al. 2003), and XCT scanned in the Woodlab at Ghent University in Belgium (Van den Bulcke et al. 2014). The scanned images were converted to mean densities of the whole core using a

reference material of known density and air with a density assumed to be zero.

Tree growth and survival

At the nine visited sites, we measured the height of every tree (Moonlight et al. 2021). For multi-stemmed trees, commonly found in TDFs, only the tallest stem was considered. Additionally, we recorded the survival status of each individual, which was evaluated by scratching the bark and observing whether the cambium displayed any signs of life (Werden et al. 2020). In the sites with multiple composite soil samples, tree individuals were related to their soil sampling zone. Absolute height growth rates (hereafter denoted as growth [m/year]) were computed by subtracting the obtained height by 30 cm, reported as the mean planting height by restoration managers, and divided by the time in years between planting and monitoring (Visser et al. 2016; Werden et al. 2020):

$$HR = \frac{Height - 30\ cm}{2022 - Planting\ year}$$

During the survival assessment, we could only evaluate the status of individuals present at the time of monitoring and hence omitted multiple empty spots, which causes an overestimation of survival rates and might potentially induce bias by favouring some species more than others.

Data analysis

Overall, ten species were present in at least two sites and are included in our analysis. For two sites established in the monitoring year (i.e. SAPET and SICH), we only evaluated survivorship, as measured heights are expected to represent planting size and not (yet) outcomes of trait-environment interactions (Visser et al. 2016), which could increase the signal-to-noise ratio and hamper capturing significant effects (Rodríguez-Alarcón et al. 2024). Across four other sites, 346 negative and 33 zero height growth rate values were removed (Werden et al. 2020), as these were likely caused by tree cutting or animal damage. Additionally, we removed all 27 growth rate observations considered to be an outlier within the site following Tukey (1977). In the end, we obtained a dataset of 5514 tree individuals for the survival assessment, which, after the removal of dead individuals, non-positive height values and two sites, resulted in 2672 height rate observations (Supplement S3). All explanatory factors, except for the

categorical nitrogen fixation, were standardized, facilitating model fitting and convergence and allowing for direct comparison of predictor effect sizes (Zuur et al. 2009).

Generalised linear mixed models (GLMMs) were then employed to evaluate the drivers of growth and survival variability in tropical dry forest restoration, with site identity as a random intercept to incorporate the ecological assumption that within-site observations are more closely related (Banin et al. 2023). Since WD and SLA were highly negatively correlated (Pearson $\rho < -0.7$), we retained only the former, as it is phylogenetically more conserved, shows less plastic variability and is not affected by the timing of the measurements (Poorter et al. 2018; Derroire et al. 2018; Slot & Winter 2017). Additionally, the ability to fix nitrogen (Nfix) was added to our model. We expanded our functional trait model with potential evapotranspiration (PET), the mean temperature in the wettest quarter (BIO8) and the presence of organic matter (OM). Due to the strong correlations between most environmental factors, we could only include a limited amount of explanatory variables. Since irrigation was anticipated to be a more significant factor in water availability than mean annual precipitation (MAP) at our restoration sites, and as MAP differed relatively little between the sites (Supplement S1), we opted to use PET as a measure of atmospheric aridity (Méndez-Toribio et al. 2020), rather than the conventional aridity index, which is calculated by dividing annual precipitation by potential evapotranspiration (Zomer et al. 2022). In addition, we included BIO8 to account for energy availability in the rainy season (Slot & Winter 2017) and OM as an indicator of soil fertility and water-holding capacity (Wood et al. 2016). Interaction effects with WD were included for all abiotic predictor factors except for BIO8, as this increased the variance inflation factors (VIFs) considerably (Kim 2019). We used the same model structure for both growth and survival rates:

$$\text{Growth (or survival)} \sim \text{Nfix} + \text{WD*PET} + \text{WD* OM} + \text{BIO8} + (1|\text{Site})$$

Height growth rates were analysed using the *lme4* package (Bates et al. 2015) with gamma error distribution and Restricted Maximum Likelihood (REML) estimation (Banin et al. 2023; Luke 2017). Significance of the results was assessed according to Satterwaite's degrees of freedom method included in the *lmerTest* package (Kuznetsova et al. 2017). Survival rates were modelled via a binomial error distribution with *cloglog* link function (Banin et al. 2023) using the *glmmTMB* package (Brooks et al. 2017). We used the *piecewiseSEM* package

(Lefcheck 2016) to compute the marginal (R^2_m) and conditional (R^2_c) coefficients of determination to assess the goodness-of-fit (Nakagawa & Schielzeth 2013; Werden et al. 2020). The former quantifies the variance explained by the fixed effects, while the latter evaluates the variance explained by both the fixed and random factors. To test the validity of our findings, we also ran the same model with SLA instead of WD (Supplement S4). Furthermore, we built a model to assess the interactive effect of BIO8 and WD, thereby omitting the interaction between WD and PET due to the high VIFs (Supplement S5). Lastly, we ran our survival model for a reduced dataset, in which the sites established in the year of monitoring were excluded (Supplement S6). These additional analyses confirmed our main results. All analyses were performed in R 4.2.3 (R Core Team 2023).

RESULTS

The performance of planted tree seedlings varied considerably between species and sites (Supplement S3) and was significantly influenced by trait-environment interactions (Table 1; Figure 2; Supplement S7). First, the interaction between WD and atmospheric aridity had a considerable influence on height growth rates. Specifically, the growth of species with a higher WD was more negatively affected by an increase in PET than that of species with a lower WD (PET x WD -0.17 $p < 0.001$). Likewise, a significant interaction existed between WD and OM, as the height growth of species with a low WD remained relatively stable across the OM gradient, while that of species with high WD decreased rapidly when OM became limiting (OM x WD 0.20 $p < 0.001$). Besides these significant interaction effects, we observed important main effects for Nfix (0.35 $p < 0.001$), WD (-0.66 $p < 0.001$), OM (0.14 $p < 0.05$), PET (-0.49 $p < 0.01$) and BIO8 (0.52 $p < 0.01$). Overall, the fixed effects in our model accounted for 56.3% of the variance in height growth (R^2_m), while adding site as a random factor increased the explained variance to 58.3% (R^2_c).

Similarly, trait-environment interactions significantly altered survival rates (Table 1 and S5; Figure 2). In particular, species with a low WD showed rapidly growing survivorship when the organic matter content increased, while survival rates of species with a high WD were less affected (WD x OM -0.13 $p < 0.001$). We also observed a significant positive interaction between WD and PET (WD x PET 0.12 $p < 0.01$). Moreover, the main effect of OM was positive (OM 0.08 $p < 0.05$), as was the case for WD (0.17 $p < 0.001$) and Nfix (0.45 $p < 0.001$). A higher

temperature in the wet season decreased the survival rate (BIO8 -0.32 $p < 0.05$). In contrast to height growth, our model could only explain limited variation in survival rates through fixed (R^2_m 3.0%) and both fixed and random effects (R^2_c 11.3%).

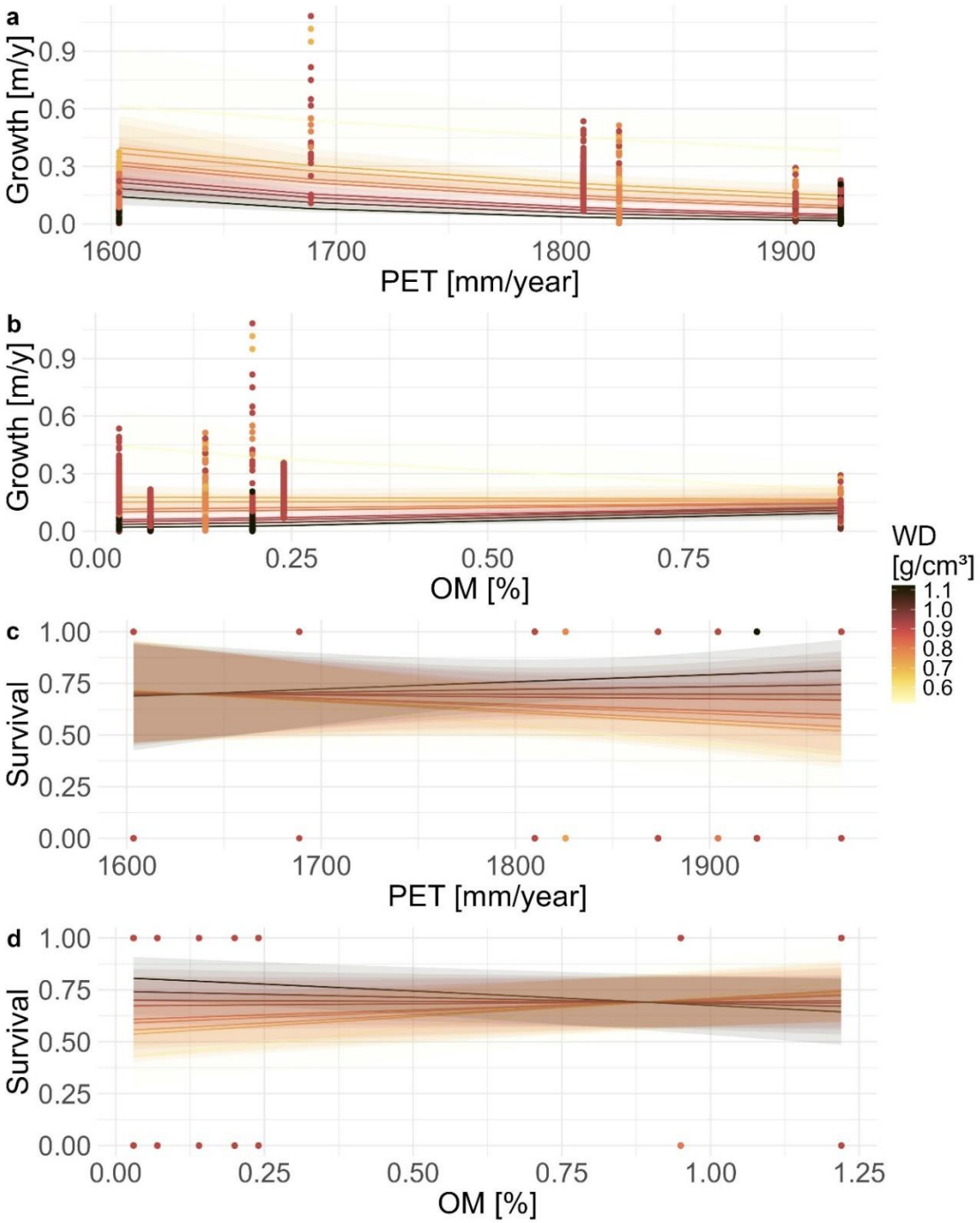

Figure 2: Significant interaction effects between wood density (WD [g/cm³]) and annual potential evapotranspiration (PET [mm/year]) (a) and WD and organic matter content (OM [%]) (b) on height growth. Effect of the interaction between WD and potential evapotranspiration (c) and between WD and organic matter (d) on survival rate.

*Table 1: Parameter estimates (β) and 95%-confidence intervals (CI) for the generalized linear mixed models (GLMMs) for height growth rate and survival rate, with nitrogen fixation (Nfix), wood density (WD [g/cm³]), organic matter content (OM [%]), potential evapotranspiration (PET [mm/year] and mean temperature in the wettest quarter (BIO8 [°C]) as predictor variables. Significance of the parameters is indicated with * p<0.05, ** p<0.01 and *** p<0.001. Goodness-of-fit is given as both marginal (R^2_m) and conditional (R^2c) coefficients of determination.*

Driver	Height growth rate		Survival rate	
	β	CI	β	CI
Nfix	0.35***	[0.28, 0.41]	0.45***	[0.38, 0.51]
WD	-0.66***	[-0.70, -0.62]	0.17***	[0.12, 0.22]
OM	0.14*	[0.08, 0.19]	0.08*	[0.04, 0.12]
PET	-0.49**	[-0.58, -0.40]	-0.08	[-0.23, 0.08]
BIO8	0.52**	[0.44, 0.61]	-0.32*	[-0.48, -0.16]
WD*OM	0.20***	[0.16, 0.24]	-0.13***	[-0.17, -0.10]
WD*PET	-0.17***	[-0.20, -0.14]	0.12**	[0.07, 0.16]
R^2_m (%)	56.3		3.0	
R^2_c (%)	58.3		11.3	

DISCUSSION

Our results demonstrate the importance of incorporating trait-environment interactions when assessing tree planting performance in restoration projects. While several of the studied environmental drivers (potential evapotranspiration (PET) and organic matter (OM)) and functional traits (wood density (WD)) independently influenced growth and survival, the presence of interactions between these drivers implies that evaluating main effects alone is insufficient to predict overall TDF restoration success.

Contrasting wood density effects on tree survival and growth rates

Our findings revealed significant but opposing effects of wood density on height growth and survival, lending empirical support to the *growth-mortality hypothesis* (Wright et al. 2010; Sterck et al. 2011) and its relevance to TDF restoration (Werden et al. 2023; Rosell et al. 2022). Specifically, conservative species with higher WD exhibited slower growth but enhanced survival, which can be attributed to their greater investment in dense leaf and wood tissues (Markesteijn & Poorter 2009). While this enables better tolerance of stress and disturbances, increasing survivorship, the strategy comes at the expense of lower resource allocation towards growth (Chave et al. 2009; Rosell et al. 2022). In addition to wood density, the ability

344 to fix atmospheric nitrogen enhanced both growth and survival rates, which confirms the
345 suggested competitive advantage of nitrogen-fixers over non-fixer species (Menge & Chazdon
346 2016). Nitrogen fixation increases foliar nitrogen contents, enabling higher photosynthetic
347 activity and water-use efficiency (Pellegrini et al. 2016; Poorter & Markesteijn 2008), and
348 supports the production of nitrogen-containing defensive compounds, thereby reducing
349 insect-induced mortality (McDowell et al. 2008; Menge & Chazdon 2016).

350 The *growth-mortality* hypothesis holds along environmental gradients

351 General resource-use theory predicts high growth and survival rates for acquisitive species
352 with a lower WD under favourable conditions, but a rapidly decreasing performance as water
353 and nutrients become limiting (Sterck et al. 2011; Baribault et al. 2012; Caleño-Ruiz et al.
354 2023). Conversely, conservative species are better able to tolerate drought or low nutrient
355 availability, resulting in high survival rates and stable – but rather low – growth along the
356 resource gradients (Chave et al. 2009; Pinho et al. 2019). Indeed, we observed conservative
357 species with higher WD to have more stable survival rates along the gradients in atmospheric
358 aridity and organic matter, here used as a proxy for nutrient content (Wood et al. 2016). This
359 supports, at least for survivorship, the theory that conservative species are more tolerant of
360 lower resource availabilities. For growth, however, we observed an opposite impact than
361 anticipated: the growth of acquisitive species decreased less rapidly along the resource
362 gradients than the growth of more conservative species. These results suggest that the
363 *growth-mortality hypothesis* holds along environmental gradients, as acquisitive species are
364 even under resource-poor conditions able to retrieve sufficient resources and allocate them
365 to height growth. Nonetheless, their resource-use strategy results in higher survivorship
366 vulnerability to dry and low nutrient conditions, indicating that few acquisitive species are able
367 to survive the harsh initial conditions in TDF restoration sites (Poorter et al. 2019; Schwartz et
368 al. 2022).

369 The high and stable growth rates of acquisitive species along the resource gradients (i.e. both
370 water and organic matter availability) are surprising and indicate that those individuals that
371 manage to establish achieve high growth rates independent of site resource availability,
372 suggesting a competitive growth advantage over slow-growing conservative species (Werden
373 et al. 2023). First, the fast-growing acquisitive species likely invest heavily in belowground

biomass and thereby increase their rooting density (Fagundes et al. 2022; Méndez-Toribio et al. 2020), which gives them an enhanced growth capacity (Werden et al. 2023) and makes them less susceptible to changes in soil fertility or atmospheric aridity (Markesteijn & Poorter 2009). Once established and with a well-developed rooting system, acquisitive species may thus retrieve sufficient nutrients and water to invest in height growth compared to conservative species. However, due to the decoupling between above- and below-ground resource-use strategies (Werden et al. 2023; Worthy et al. 2020), we are not able to confirm this hypothesis due to the lack of root trait data, although it is supported by other studies reporting a relationship between acquisitive resource use and rooting density (Comita & Engelbrecht 2009; Méndez-Toribio et al. 2020). Secondly, the stable growth of acquisitive species along the resource gradient can also be explained by their high growth rates during the short wet season (Mendivelso et al. 2014; Poorter et al. 2018), after which many of them quickly shed their leaves to avoid drought stress (Fagundes et al. 2022; Poorter & Markesteijn 2008), making the effect of atmospheric aridity (high PET) on height growth less relevant (Rodríguez-Alarcón et al. 2024). Conservative species, on the other hand, remain active in (part of) the dry season, extending their growing period but also increasing their susceptibility to higher evaporative demand (McDowell et al. 2008; Wright et al. 2010). This forces them to adapt their growth rates to existing conditions, resulting in a higher sensitivity to potential evapotranspiration.

Acquisitive species benefit more from higher wet season temperatures

Higher temperatures in the wettest quarter decreased survivorship but positively affected growth rates. While the negative effect on survival rates aligns with our expectations, as higher temperatures can exacerbate drought and hydraulic failure (McDowell et al. 2008), the positive effect on growth rates is surprising and contradicts previous studies (Méndez-Toribio et al. 2017; Mendivelso et al. 2014). In TDFs, however, higher temperatures during the growing season can benefit tree growth by enhancing energy availability, thereby increasing photosynthetic activity (Slot & Winter 2017). In addition, we anticipated that acquisitive species would be more sensitive than conservative species to temperature increases, with rapidly decreasing performance under warmer conditions (Sastry & Barua 2017). Although we could not include this interaction in our main model due to high VIFs, testing it separately

revealed that growth rates of acquisitive species actually increased more rapidly along the temperature gradient than was the case for conservative species. While this contradicts our initial expectations, it supports the hypothesis by Slot and Winter (2017) that acquisitive species benefit more from increased energy availability, likely due to their higher electron transport capacity and larger temperature-response plasticity. It also corroborates our hypothesis that acquisitive species are less sensitive to high atmospheric aridity by focusing on achieving high growth rates in the favourable, wet period with sufficient water and energy availability.

Study limitations and future research avenues

Overall, our results indicate that the *growth-mortality* hypothesis holds along resource gradients, with acquisitive species able to sustain their high growth rates even when water or nutrient content becomes limiting, although they exhibit higher vulnerability to mortality under these conditions compared to conservative species. Despite the importance of this empirical evidence supporting the significance of trait-environment interactions on seedling performance in restoration projects, several limitations must be considered. First, survival rates might be biased as we could only include remaining dead individuals with certain species identification and had to omit empty planting spots, which may have resulted in an overrepresentation of conservative species with more durable stems (Chave et al. 2009). This could also explain the low explanatory power of the survival model. Nonetheless, our results align with our expectations and are corroborated by previous studies (Wright et al. 2010; Díaz et al. 2004). Second, the observational nature of our study prevented the assessment of key management strategies in TDF restoration, such as irrigation (Dimson & Gillespie 2020), which could have influenced seedling performance. However, our use of potential evapotranspiration as a proxy for atmospheric aridity provided an indirect measure of drought stress (Méndez-Toribio et al. 2020), independent of management interactions. Third, we could only incorporate one functional trait in our models. While incorporating multi-dimensional trait axes could potentially improve explanatory power (Matlaga et al. 2024; Rodríguez-Alarcón et al. 2024), our results remained consistent when substituting WD with SLA, probably due to their strong correlation, further reinforcing our conclusions.

Future research on trait-environment interactions should focus on experimental studies

across resource gradients in the Tumbes-Piura TDFs, using a study design with known initial species numbers and standardised management practices. Furthermore, we encourage future restoration research to incorporate trait plasticity (Derroire et al. 2018; Poorter et al. 2018) and ontogenetic variability (Metz et al. 2023; Poorter & Markesteijn 2008), since they both enable individuals to acclimate to local abiotic conditions and hence might influence trait-environment interactions in restoration projects (Lanuza et al. 2020; Worthy et al. 2020). Additionally, accounting for the high soil and microclimatic heterogeneity of TDFs in future studies can shed additional light on the importance of trait-environment interactions in restoration practices (Rodríguez-Alarcón et al. 2024; Caleño-Ruiz et al. 2023; Schwartz et al. 2022).

Given our observation that seedling performance depends on the interaction between environmental variables and species' functional traits, our findings underscore the importance of context dependence in restoration projects and highlight that species selection should depend on both the site's environmental conditions and overarching restoration objectives (Zirbel & Brudvig 2020; Fremout et al. 2022). This study lays the foundation for future research on these interactions, particularly within the underexplored Tumbes-Piura TDFs.

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