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Acquisitive traits improve seedling survival with reduced soil moisture at the edges of a fragmented tropical forest

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Abstract

Climate change and habitat fragmentation threaten biodiversity, but their interactive effects remain poorly understood. In closed-canopy forests, altered rainfall patterns may induce drought conditions that are exacerbated at forest edges due to warmer, drier microclimates. Plant responses to water limitation can be mediated by functional traits related to resource acquisition and stress tolerance. We examined how reduced soil moisture and edge conditions jointly affect seedling survival, and whether species' responses are explained by their traits. In a human-modified forest in the central Western Ghats, India, we transplanted ~ 1-year-old seedlings in a factorial combination of habitat (forest edge vs. interior) and moisture deficit (throughfall exclusion vs. control). We monitored survival through one year and estimated moisture response (survival in throughfall exclusion vs. control) and tested its relationship with six traits. Throughfall exclusion reduced soil moisture more at edges, particularly during dry months. At the edge, three species showed significantly lower survival under drought, whereas survival in the interior did not differ with water treatment. Acquisitive traits (low stem specific density, low leaf dry matter content, and low leaf mass per area) improved survival with reduced moisture at edges. Trait-mediated responses were not evident in the interior, likely due to buffered microclimates. Multi-trait combinations were better predictors of moisture response than individual traits, indicating trait coordination. Our results suggest that drier conditions may favour acquisitive species at forest edges, which has implications for community composition, management and restoration of fragmented forests in a changing climate.

Keywords Tropical forests · Forest fragmentation · Seedling survival · Trait-environment interactions · Resource acquisition

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Introduction

Climate change and habitat fragmentation pose pressing threats to global biodiversity, and their interactive effects need to be understood better (Haddad et al. 2015; Weiskopf et al. 2020). Rising temperature and altered precipitation patterns are projected to result in droughts, which can increase plant mortality (Duffy et al. 2015; Allen et al. 2017). Even in moist biomes, plant species performance relates to water availability (Engelbrecht et al. 2007; Comita and Engelbrecht 2009; Esquivel-Muelbert et al. 2019; Krishnadas et al. 2021), and lower moisture will affect species to differing extents. The impact of reduced moisture on plant performance may be modulated by other global change factors, an example being habitat fragmentation. Forest fragmentation creates edge habitats that differ significantly from forest interiors, with greater light availability, higher temperatures, reduced humidity, high vapour pressure deficit and altered soil conditions. These abiotic changes can alter plant performance at edges (De Frenne et al. 2015; Krishnadas et al. 2019; Zellweger et al. 2020). During dry times, edge effects may act synergistically, intensifying water stress through warmer, drier microclimates and reduced soil moisture retention.

While water deficit can harm plants at all life stages, seedlings are particularly vulnerable due to their shallow root systems and limited stored resources in the light-limited understory conditions for growth and survival (Comita and Engelbrecht 2014; Engelbrecht et al. 2007). Seedling establishment and community composition are affected by edge effects in forest fragments (Krishnadas and Comita 2018; Krishnadas et al. 2019, 2020; Krishnadas 2023), thought to be due to changes in light availability, but the role of moisture availability in mediating species responses is not well established. Since the seedling bank is critical for forest regeneration, understanding how reduced moisture interacts with fragmentation to shape species performance would help predict future regeneration (Engelbrecht and Kursar 2003; Poorter and Markesteijn 2008; Markesteijn and Poorter 2009; O'Brien et al. 2015).

Plants cope with environmental stress through functional traits that relate to resource acquisition and stress tolerance (Krishnadas et al. 2025). Traits such as high leaf mass per unit area (LMA), high stem and root specific density (respective organs' dry mass/fresh volume), and low leaf area (LA) are often associated with moisture deficit tolerance through reduced transpiration, enhanced tissue rigidity, or slow resource use (Poorter and Markesteijn 2008; O'Brien et al. 2017a; Krishnadas et al. 2021). However, trait–function relationships are not always straightforward—for example, thick leaves may function in either water conservation or water storage depending on anatomy and context (Chaves et al. 2003). Thus, empirical data are essential to test how traits mediate moisture deficit response in situ, where multiple drivers act simultaneously on plant performance.

Tree species with higher wood density survived better during drought in tropical forests (Phillips et al. 2009; Van Nieuwstadt and Sheil 2005; O'Brien et al. 2017a),in the Mediterranean (Martínez-Vilalta et al. 2010) and temperate forests (Martinez-Meier et al. 2008; Nardini et al. 2013). Denser wood corresponds to general stress tolerance, and in the case of drought, higher wood density may be associated with better cavitation resistance. By comparison, a regional assessment of species distributions in peninsular India found that species with lower wood density and higher LMA increased with greater seasonal water deficit, suggesting a fitness advantage for these traits in drier conditions (Krishnadas et al. 2021). While the LMA patterns reflect the expectation that species with conservative resource use are favoured in drier sites, patterns for wood density contrast with global expectation, and may have been driven by species deciduousness.

Less is known about how traits influence moisture deficit responses at earlier life stages. Greenhouse studies suggest that xylem structure and stomatal traits influence moisture response of seedlings; larger xylem conduits reduced growth and photosynthesis, and smaller stomata decreased survival rates in reduced moisture relative to well-watered controls (Jhaveri et al. 2024). In another experiment on seedling responses to light and water limitation, water deficit was found to shift biomass allocation towards roots at the expense of leaves (Sunny et al. 2025). In addition to controlled greenhouse experiments that provide valuable insights into seedling responses to moisture, complementary insights can be gained by assessing plant response to reduced moisture in natural conditions where plant-water relations can be regulated by competition, water lift, or variable soil resource availability (Comita and Engelbrecht 2014).

To understand how reduced soil moisture and edge effects together shape seedling performance in field conditions, we used throughfall exclusion to simulate moisture deficit at the edges and interiors of forest fragments in a human-modified landscape in the Western Ghats biodiversity hotspot in southern India. The region overall has experienced significant deforestation, with 20% annual loss in forest cover, decreasing patch size, and increasing edge density from 1975 to 2005 (Reddy et al. 2013), which makes it opportune and necessary to examine the interaction between reduced moisture and forest fragmentation. Specifically, we asked:

1. Does rainfall exclusion decrease soil moisture availability and properties by a greater extent at forest edges than interiors?
2. Does the effect of moisture deficit on the survival of forest seedlings vary between the forest edge vs. interior?
3. Do plant traits mediate the moisture response of seedlings at forest edge vs. interior?

We hypothesised that reduction in soil moisture would be more pronounced at forest edges, possibly due to greater solar radiation and wind exposure. We expected seedling survival to decrease with moisture deficit on average, and more so at edges due to harsher microclimatic conditions. Finally, we predicted that traits associated with resource-conservative strategies, such as thicker leaves and denser stems and roots, would show smaller declines in performance under moisture deficit in this humid forest, and the influence of traits would be more prominent at forest edges. Although thick leaves can sometimes function as water storage, in this system we expected higher LMA and tissue density to primarily reflect a conservative water use strategy that slows water loss and enhances survival during moisture stress, particularly at the forest edge.

Methods

Study site

This experiment was conducted in a 30 km^2 human-modified forest landscape in the central Western Ghats (12°56'N, 75°39'E), located in the Hassan district of Karnataka state, India (Krishnadas et al. 2018). The landscape comprises tropical humid forests and receives an annual rainfall of ca. 5000 mm, most of which falls during the monsoon season from July through October, with a pronounced dry season from December through May. Most seedling recruitment occurs during or just after monsoon rains, but seedlings have to survive the dry season to persist. Forest fragments make up ca. 60% of the study landscape, with the remainder being tea plantations, human settlements, and montane grasslands. The soils are primarily clayey Alfisols with good drainage, originating from a gneissic base.

Experimental design

We conducted this study on seedlings of 16 native tree species (Table S1). Species were chosen according to their occurrence in this landscape, availability and germination of sufficient seeds in local nurseries, and a sufficient degree of shade-tolerance for seedling survival in the understory. Seeds were sown in plastic growbags and emergent seedlings cultivated for 9–12 months after germination, then transplanted into the field between January and February 2021. Each focal seedling in the experiment was tagged with a unique ID and planted within a 3 m X 2 m plot in the pairwise combination of control and moisture deficit treatments at the forest edge and interior, replicated across 13 locations (hereafter blocks). We cleared any pre-existing seedlings and planted one individual of each of 16 species into each plot randomly. After an acclimation period, moisture deficit treatment was simulated using the throughfall exclusion technique by covering the assigned plot with polycarbonate sheeting to prevent rain from falling onto seedlings and the underlying soil layers. This method has been successfully used in multiple reduced moisture studies across the world and shown to reduce soil moisture without compromising light availability (Engelbrecht and Kursar 2003; O'Brien et al. 2017b). The throughfall exclusion was maintained from March 2021 to February 2022. We left the leaf litter intact in plots at the start of the experiment and for the throughfall exclusion plots, we periodically (every 2 weeks) added leaf litter equivalent to the adjacent litterfall. Through the course of the experiment, we removed any naturally recruiting seedlings.

In each plot, soil moisture was measured every month using a hand-held volumetric soil moisture sensor (HS2-20-HS2 CSA, Hydrosense II). Three measurements for each plot were taken at a depth of 20 cm as we expected the one-year-old seedlings to access the water from shallow depths. Tagged seedlings were assessed monthly for their status (alive/dead), height, and production of new leaves. At the end of the experiment, soil samples from the top 20 cm were collected from the corners of each plot to analyse soil physical (pH, and Electrical conductivity) and chemical (Organic Carbon, Available Cu, Mn, Fe, Zn, K, and P) properties.

Trait data

We followed protocols recommended by Pérez-Harguindeguy et al. (2013) to quantify functional traits. We assumed that the traits do not vary within a year of the experiment between the edge and the interior. Three to five alive individuals from both the forest edge and interior of each species were harvested, brought back to the field station on the same day, and saturated overnight by immersing the petiole, root, and branch in a container filled with water. Water-saturated leaves were weighed to determine fresh weight, scanned with a desktop scanner for quantifying leaf area (LA), and then oven–dried at 70 °C for 72 h to determine dry weight. Leaf mass per unit area (LMA) was quantified as the ratio of dry weight to area, and leaf dry matter content (LDMC) as the ratio of dry weight to saturated fresh weight. A portion of the stem, main root and fine root were taken, and the water displacement method was used to estimate the volume, followed by oven-drying at 70 °C for 72 h to determine dry weight. Stem-specific density (SSD) was estimated as the ratio of dry weight to volume. Main root specific density (MRSD) and fine root specific density (FRSD) were estimated as the dry weight of the main root and fine root to their volumes.

Statistical analysis

For question 1, linear mixed effects models with beta error distribution were used to model soil moisture percentage in relation to an interaction between habitat and treatment. Plot ID and month were included as random intercepts. Random slopes were modelled for each month to capture temporal dependence of responses. Similarly, we checked whether throughfall exclusion altered the physical and chemical properties of the soil by the end of the experiment. We first did a Principal Component Analysis (PCA) on soil parameters to reduce dimensionality and account for correlation among parameters. We then used a linear mixed effects model with Gaussian error distribution to relate the first two PCA axes (PC1 and PC2) as well as each individual soil parameter to interaction between forest habitat and treatment, with plot ID included as a random intercept.

For question 2, we assessed the survival of individual seedlings using a generalised linear mixed-effects model with a binomial error distribution. Fixed effects tested whether survival response to moisture deficit varied between forest edge and interior habitat, while random intercepts and slopes for the interaction of effect and treatment were included per species to account for species-specific response to habitat and treatment. Inference for random slopes of species between control and moisture deficit treatment were made using the overlap of CI in one treatment factor with the estimate of another treatment factor (Cumming et al. 2007).

For question 3, we quantified the moisture deficit response of each species as the proportion of individuals surviving in the throughfall exclusion treatment relative to the control at the end of the experiment across all locations (Engelbrecht and Kursar 2003). This approach allowed us to attribute edge vs. interior differences specifically to water, even as other factors (e.g., light) may be involved in plant performance.

$$
\begin{aligned}
&Moisture\ Deficit\ Response \\
&= Number\ surviving\ in\ moisture\ deficit\ treatment \\
&/Number\ surviving\ in\ control
\end{aligned}
$$

To test if traits mediate response to moisture deficit, first, we did a principal component analysis (PCA) on traits to obtain composite phenotypes defined by trait combinations based on leaf mass per area, leaf dry matter content, leaf area, stem specific density, main and fine root specific density. To test whether the composite phenotype defined by PCA axes and individual plant traits correlates with moisture deficit response, and if this relation differed between forest habitats, we used linear mixed-effects models with gamma error distribution. Gamma errors were suitable as the responses varied from 0 to 2.5. Species identity was included as a random intercept, accommodating species-specific variation additional to measured traits. To understand habitat specific trait interactions, we used post-hoc contrasts with the glht function for the 5th and 95th quantile of each measured traits and used. We also studied this question with the binomial survival data as a function of traits, treatment and forest habitat with a three-way interaction. We also tested if individual survival was mediated by trait interaction with forest habitat and treatment using generalised linear mixed-effects models (GLMMs) with a binomial error distribution and a logit link function, as survival was measured as a binary outcome (alive or dead). The fixed effects included plant trait values, forest habitat (edge vs. interior), and moisture deficit treatment (control vs. throughfall exclusion). Species identity was included as a random effect, with random slopes for forest habitat and moisture deficit treatment to account for species-specific responses.

All data management and analysis were conducted using the R programming language version 4.3.1 (R Core Team 2023). Mixed effects models were implemented using glmmTMB (Brooks et al. 2017) and visualised using ggplot2 (Wickham et al. 2007), FactoMineR (Lê et al. 2008), and sjPlot (Lüdecke 2013). Summary of the tested hypothesis and models used are provided in the supplementary information (Table S2).

Results

Soil moisture, physical and chemical properties

The lowest soil moisture (VWC) was observed in the month of January with values of 5.02% ± 0.52, 7.21% ± 0.6, 7.56% ± 0.56, and 8.47% ± 0.78 in the forest edge moisture deficit treatment, forest edge control, forest interior moisture deficit treatment and forest interior control respectively (Table S3, Fig. 1). The highest soil moisture was observed in the month of August for the control treatment at both forest habitats, whereas moisture deficit treatments at the forest edge and interior experienced highest soil moisture in the month of September and July respectively. The highest soil moisture values (VWC) observed were 16.02% ± 1.48, 32.95% ± 0.59, 20.17% ± 1.45, and 34.82% ± 0.93 in the

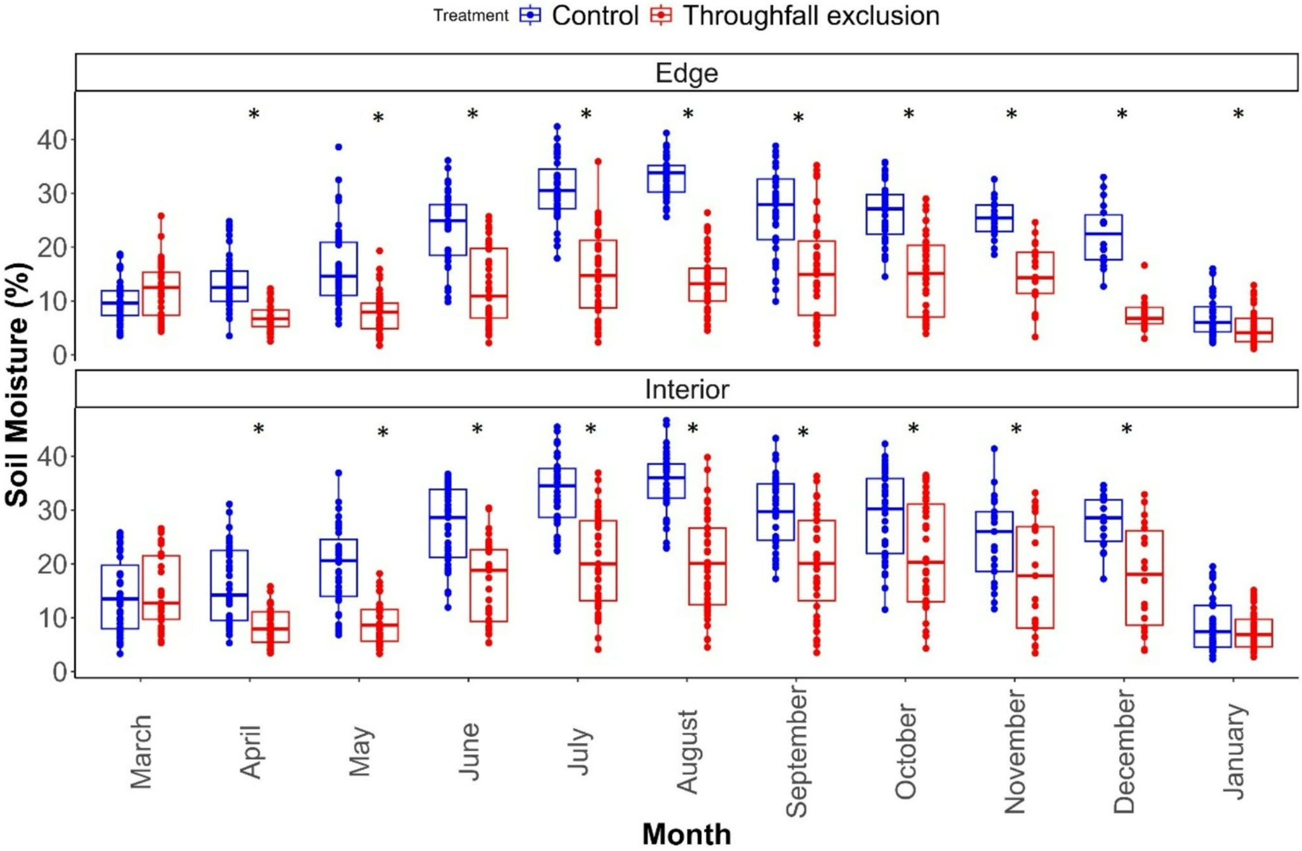

Fig. 1 Soil moisture recorded across habitats (edge & interior) and treatments (control & Throughfall exclusion). Soil moisture percent was modelled using a generalized linear mixed-effects model with a beta error distribution. Plot identity was included as a random intercept, and treatment was modelled as a random slope within month to account for temporal variation in moisture responses. Upper and lower panel shows the soil moisture percentage variation in edge and interior respectively. Blue and red colour represents control and throughfall exclusion treatment respectively. * Indicates significant difference between treatments with alpha ≤ 0.05

edge-moisture deficit treatment, edge-control, interior-moisture deficit treat treatment and interior-control, respectively. As expected, throughfall exclusion significantly reduced soil moisture over a year, with a stronger effect at the forest edge than in the interior. At the edge, soil moisture content halved under moisture deficit treatment, decreasing from 20% (95% CI: 15–26%) in control plots to 10% (8–13%) in moisture deficit treatment plots. In contrast, in the forest interior, soil moisture declined by approximately 32%, from 22% (17–29%) in control to 15% (12–19%) under moisture deficit treatment (Fig. S1). These results indicate that the impact of throughfall exclusion on soil moisture availability is more pronounced at forest edges compared to interiors. Monthly values across the factor types showed that moisture decreased in the throughfall treatment for all the months except March in the forest edge and March and January in the forest interior (Table S4, Fig. 1).

Principal Component Analysis (PCA) of soil physical and chemical properties showed that the first two principal components together explained 51.0% of the total variance, with Dim1 and Dim2 accounting for 29.3% and 21.7%, respectively (Fig. S2). Dim1 was primarily associated with organic carbon (Org_C), electrical conductivity (E_cond), pH, and available potassium (Available_K), while Dim2 was mainly influenced by micronutrients such as available manganese (Available_Mn), zinc (Available_Zn), and iron (Available_Fe). Available copper (Available_Cu) and phosphorus (Available_P) contributed moderately to both dimensions but were more aligned with Dim1. However, our analysis found no significant differences in soil physical (pH and electrical conductivity) and chemical (organic carbon, and available Cu, Mn, Fe, Zn, K, and P) properties between the treatments of both forest edge and interior (Table S5).

Seedling survival

The predicted survival probability of seedlings was 80%, 73%, 73% and 75% in edge control, edge moisture deficit treatment, interior control and interior moisture deficit treatment, respectively. Seedling survival probability decreased by 8.75% between control and moisture deficit treatment in the forest edge, but was not statistically significant (Fig. S3, Table S6). However, species-specific slopes showed substantial variation in moisture deficit responses, with three species having significantly lower survival under moisture deficit treatment at the forest edge (Fig. 2, Table S7): *Artocarpus heterophyllus (ARTHET)*, *Artocarpus hirsutus (ARTHIR)*, *and Calophyllum apetalum (CALAPE)*. Survival differences between control and moisture deficit treatment were less pronounced in the forest interior, with no species showing strong treatment-specific declines.

Traits and moisture deficit response at forest edge vs. interior

The first two axes of the Principal Component Analysis (PCA) explained 65% (Fig. S4) of the total variation in traits for the 16 species (PC1: 46.4%, PC2: 18.6%). LMA, LDMC, SSD, MRSD were positively loaded with PC1, and Leaf area was negatively loaded on PC1 indicating a resource acquisitive vs. conservative dimension. Only FRSD was positively loaded on PC2. For response to moisture deficit, results were largely consistent between analyses of trait-mediated individual survival and survival ratios. We chose to present survival ratios as they capture the aggregate species-level response in relation to mean trait values. Outputs from models analysing individual survival are available in the Supplementary Information (Table S8, Fig. S5). In the trait-mediated survival ratio, we kept interior as a baseline and in the results that follow, coefficients from the gamma regression and their 95% confidence intervals are presented on the exponentiated scale, where values less than 1 indicate a negative relationship and values greater than 1 indicate a positive relationship (Table 1). The Tuckey contrasts for the habitat-specific trait interactions results, along with their coefficients in log scale and significance levels, are presented in Table S9.

Although soil moisture decreased significantly with throughfall exclusion in both edge and interior, trait mediated response was more prominent in forest edge. Multi-trait phenotypes (principal component axes) showed that in the interior neither multi trait phenotypes nor the individual showed significant trend with moisture deficit response (Table S9, Fig. 3). At the edge, moisture deficit response had a significant negative correlation with PC1 ($\beta = -0.53$, $p = 0.002$) and marginally negative correlated with PC2 ($\beta = -0.34$, $p = 0.07$). Individual traits showed patterns consistent with the PC axes (Fig. 3). At the forest edge, moisture deficit response showed negative trends with LDMC ($\beta = -0.48$, $p = 0.03$), SSD ($\beta = -0.57$, $p = 0.01$) and LMA ($\beta = -0.52$, $p = 0.01$). Thus, higher LMA, LDMC, and SSD, corresponding to resource-conservative strategies, were associated with greater detriment due to reduced moisture at the forest edge. Root traits (MRSD and FRSD) and LA did not influence moisture deficit response.

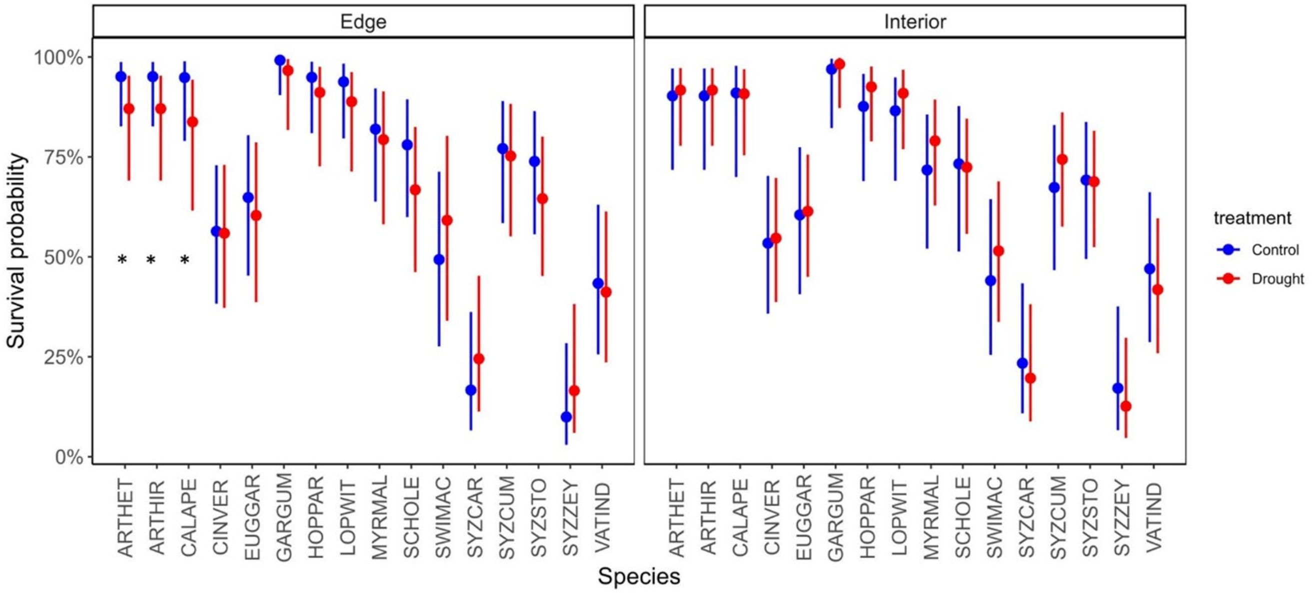

Fig. 2 Predicted survival of native tree seedlings across locations (edge and interior) and treatments (control and throughfall exclusion). Survival (binary: alive or dead) was modelled using a generalized linear mixed-effects model with a binomial error distribution. Species identity was included as a random intercept, and random slopes for treatment and location were modelled per species to account for species-specific responses. Left and right panels show the predicted survival probabilities across treatments for each species in edge and interior habitats, respectively. Blue and red colors represent control and throughfall exclusion treatments. Asterisks (*) indicate statistically significant differences between treatments ($\alpha \leq 0.05$)

Table 1 Trait-mediated moisture deficit response of species

Model	Intercept (Interior)	Edge	Trait effect at interior	Trait effect at edge
PC1	1.04 (0.93–1.17)	0.94 (0.83–1.06)	1.01 (0.94–1.09)	**0.88 (0.82–0.95)**
PC2	1.04 (0.93–1.17)	0.94 (0.83–1.06)	1.02 (0.91–1.14)	**0.89 (0.79–1.00)**
LMA	1.11 (0.79–1.56)	1.46 (0.89–2.38)	0.91 (0.53–1.55)	***0.49 (0.23–1.04)***
LDMC	1.02 (0.66–1.57)	***1.74 (0.95–3.22)***	1.09 (0.29–4.05)	**0.14 (0.02–0.90)**
LA	1.15 (0.83–1.59)	**0.63 (0.41–0.98)**	1.00 (1.00–1.00)	1.00 (1.00–1.01)
SSD	0.87 (0.61–1.25)	**1.92 (1.23–2.98)**	1.44 (0.72–2.88)	**0.24 (0.10–0.55)**
MRSD	1.01 (0.66–1.56)	1.23 (0.63–2.41)	1.09 (0.39–3.06)	0.51 (0.10–2.57)
FRSD	0.97 (0.78–1.22)	1.17 (0.86–1.58)	1.20 (0.63–2.26)	0.48 (0.20–1.15)

Moisture deficit response, quantified as the number of seedlings surviving in drought relative to control, was modelled as an interaction of plant functional traits and forest habitat (Edge and Interior) using generalized linear mixed effect model using gamma family and log link. Table contains exponentiated estimates, CIs written in parenthesis. CI values range having 1 means non-significant, range greater than one represents positive significant and range less than 1 represents significant negative correlation. Significant relationships with alpha≤0.05 were written in bold and significant relationships with alpha≤0.1 were written in bold and italics

Discussion

Both forest edge and interior habitats experienced declines in soil moisture with throughfall exclusion compared to controls, but the decrease was more pronounced at the forest edge. Soil moisture at the edge halved from 20% to 10% volumetric water content (VWC), while the interior saw a smaller decrease from 22% to 15% VWC during the experiment. This hints at forest edges exacerbating moisture stress compared to forest interiors, likely due to their increased exposure to environmental extremes such as higher light and temperature. Of course, the degree of soil moisture decrease with complete throughfall exclusion does not reflect real outcomes of diminished rainfall and only serves as a qualitative indicator of the edge-interior variation in moisture. Real-time monitoring of soil moisture and microclimate will reveal the extent to which interannual variation in climate alters moisture conditions at forest edges vs. interiors.

Interestingly, the strongest impacts of throughfall exclusion treatment were observed during the monsoon months, when soil moisture levels are typically highest under natural conditions. Drier-than-usual monsoons may therefore alter the spatial availability of soil moisture, at least at the top layers. This has implications for seed germination and seedling establishment since most tree species depend on the wetter months for their regeneration in the humid forests of the Western Ghats. Moisture deficit may also alter biotic interactions, such as microbially-mediated germination or plant performance, and needs further study (Dudenhöffer et al. 2018; Milici et al. 2025). Response to reduced moisture may also depend on seedling neighbourhoods, and moisture deficit may alter the relative importance of intra- vs. interspecific competition for seedling establishment and persistence (O'Brien et al. 2017c; Lebrija-Trejos et al. 2023).

Moisture deficit did not affect mean seedling survival even at the forest edges, where we expected prominent declines in survival, with the soil moisture dropping as low as 10%. One potential explanation is the ability of seedlings to adjust physiologically or modify resource allocation to cope with temporary moisture stress in this humid forest (Sunny et al. 2025). Also, in field conditions, the effects of reduced soil moisture may be alleviated by other factors such as plasticity in root allocation or hydraulic lift by larger trees. Seedlings may have accessed water from deeper soil layers below the 20-cm depth we measured and this may help most in the edge. This is also supported by our results of three species having difference in survival between control to throughfall exclusion treatment at the edge but not interior. Alternatively, the duration of moisture deficit may not have been sufficient to cause mortality, and effects may emerge only over longer time frames of multiple dry seasons. However, our results suggest that early, establishing seedlings that primarily access water from shallow soil layers would be more vulnerable to moisture deficit at forest edges, which may alter regeneration dynamics. Seedling performance could have been driven by moisture-induced changes in soil physical properties (e.g., pH and electrical conductivity) or chemical properties (such as organic carbon and available nutrients), but these properties did not vary between throughfall exclusion treatment and well-watered conditions at the end of the experiment.

In the forest interior, even as soil moisture dropped by 32% compared to control, moisture deficit did not alter mean survival (Table 1, intercept), and there was no discernible trait-based filtering with moisture deficit. It happened only at the edge, where throughfall exclusion decreased moisture availability more substantially than interiors. At edges, acquisitive traits—lower LMA, LDMC, and SSD—supported better seedling survival with moisture deficit. This pattern suggests that trait-mediated filtering occurs beyond a threshold level of moisture deficit. Acquisitive phenotypes (lower SSD/LMA/LDMC) survived soil moisture deficit better than conservative phenotypes. Surprisingly, root traits (MRSD and FRSD) played no role in explaining seedling

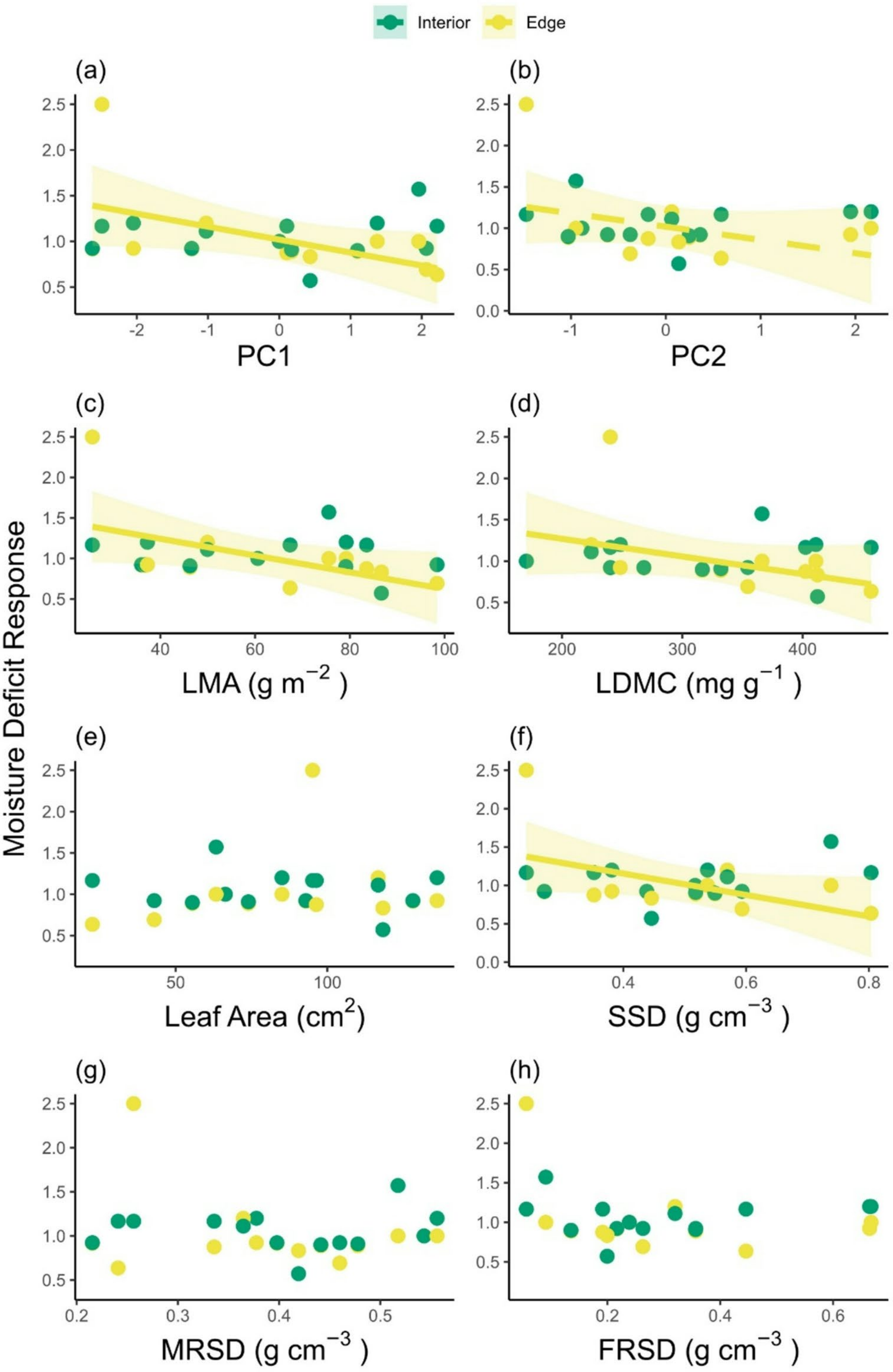

Fig. 3 Relationship between seedling moisture deficit response and functional traits at edge vs interior. Aggregate moisture deficit response, measured as the ratio of individuals surviving in drought relative to control conditions, was modelled as a function of composite and individual traits using linear mixed-effects models with a gamma error distribution. Forest habitat and trait values were included as fixed effects, and species identity was included as a random intercept and as random slopes for species responses to moisture and forest habitat. Panels show drought response as a function of: (**a**) PC1 and (**b**) PC2 from a principal component analysis (PCA) of six traits; (**c**) leaf mass per area (LMA); (**d**) leaf dry matter content (LDMC); (**e**) leaf area; (**f**) stem specific density (SSD); (**g**) main root specific density (MRSD); and (**h**) fine root specific density (FRSD). Lines indicate model fits, with bold solid lines for significant relationships ($p < 0.05$), bold dashed lines for marginal significance ($p< 0.1$) trends. Green and yellow colour circle points represent drought response at forest interior and edge respectively

response to moisture deficit. Responses to changes in soil moisture may be driven by root traits that offer tighter mechanistic links to below-ground resource acquisition, such as specific root length. The lack of trait effects in interiors may be on account of better buffering than edges from other abiotic stressors, e.g., wind, temperature, and vapour pressure deficit (VPD). While our experimental design allows to specifically link traits to moisture deficit (survival in throughfall relative to control), light availability may have affected seedling responses at the forest edge. However, ongoing work in this landscape shows that light availability does not significantly differ with distance from the edge (Jhaveri et al., in review), and we placed our experimental plots close to the permanent transects where light availability was measured to correlate with seedling demography. Similarly, herbivory was considered a possible confounding factor. In the same study (Jhaveri et al., in review) that looked primarily at impacts of herbivory and how they vary with distance from edge (without drought), did not see a difference in herbivory for planted seedlings in edge vs. interior or naturally growing seedlings in an edge-to-interior gradient. Vapour Pressure Deficit, dryness of the air that drives water loss from leaves, may have a direct bearing on trait-mediated plant response to moisture, which we did not measure. VPD is typically higher and more variable at forest edges, and recent study on the role of VPD on tropical saplings shows that even moderate increases in VPD (+0.7 kPa) can reduce stomatal conductance, growth, and water-use efficiency in saplings (Middleby et al. 2024). Recording microclimate variation and measuring anatomical and physiological traits may offer a clearer link to trait-mediated filtering with drought in human-modified forests.

Conclusion

Overall, our findings are consistent with larger-scale patterns in the Western Ghats, which found that species with lower stem-specific density (SSD) were more likely to occur in areas with greater seasonal water deficit (Krishnadas et al. 2021) – aligning with our result that acquisitive, light wooded species had higher survival with reduced moisture at forest edges. Trait-mediated filtering was stronger at edges compared to forest interiors. Where water availability fluctuates considerably over short time frames, avoiding lower moisture through rapid uptake may be more beneficial than tolerating extended dry periods (Chaves et al. 2003; McDowell et al. 2008), especially in humid environments. Our results indicate that drought in humid tropical forests can favour the regeneration of light-wooded, low LDMC species at forest edges, and may contribute to patterns of arrested succession or drive extinction debts in slower-growing tree species in fragmented forests (Silva Da Costa et al., 2020; Zuñe-da-Silva et al. 2022). The trait-based filtering we found at the seedling stage may therefore scale up to longer-term shifts in forest composition.

Given ongoing forest fragmentation, restoration efforts across tropical landscapes like the Western Ghats need to incorporate microhabitat variation and functional traits into restoration planning. Specifically, restoration strategies may need to prioritise species resilient to dry soils at forest edges to ensure successful regeneration, even under relatively closed canopies. Resource-conservative species should be planted in cooler microclimates to ensure better outcomes. Long-term monitoring across life stages and quantifying physiological traits relevant to VPD and water use may help predict restoration outcomes under increasingly variable climates. As fragmentation and climate change continue to reshape tropical ecosystems, trait-based frameworks offer a valuable tool for conservation and restoration (Laughlin 2014).

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Author contributions Peddiraju Bandaru: Data curation (equal); formal analysis (equal); investigation (equal); validation (equal); visualisation (equal); writing – original draft (equal); writing – review and editing (equal). Lakshmipriya Cannanbilla, Ashish Nambiar, Rishanth Kuruvankunath Ravi, Ashok Kumar Mani, Saravana Karuna Moorthy S, Sharath Prakash, Ranjana Gauri Muniraja, and Malavika Kamath: Experimental setup (equal), investigation (equal), Data curation (equal). Meghna Krishnadas: Conceptualization(lead); data curation (equal); formal analysis (equal); funding acquisition (lead); experimental setup (equal); investigation (equal); methodology (lead); project administration (lead); resources (lead); supervision (lead); validation(lead); visualization (equal); writing – original draft (equal); writing– review and editing (equal).

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Data availability Data and code can be found at https://github.com/Peddiraju14/Kadumane-NG.

Declarations

Competing interests The authors declare no competing interests.

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