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Effect of soils from forests and fire-deforested areas on sapling development of native tree species from a tropical montane forest

Emili A. Jimenez

miliejz86@gmail.com

Universidad Mayor de San Andrés

Daniela Ramos-Chuquimia

Universidad Mayor de San Andrés

Sara Morales

Universidad Mayor de San Andrés

Sebastián Tello

Missouri Botanical Garden

Carla Maldonado

Missouri Botanical Garden

Isabell Hensen

Martin Luther University Halle- Wittenberg

Silvia C. Gallegos

Herbario Nacional de Bolivia, Universidad Mayor de San Andrés

Research Article

Keywords: Bracken, Fire, Growth, Nutrients, Saplings, Restoration

Posted Date: August 20th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10679664/v1

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Additional Declarations: No competing interests reported.

Abstract

Tropical montane forests' biodiversity is threatened by fires that frequently promote the invasion of bracken fern (*Pteridium* spp.), hindering forest regeneration and altering soil nutrient dynamics. Although bracken can favor early tree seedling recruitment, seedling growth and sapling development may remain slow due to post-fire soil degradation or other limiting factors. We disentangled the effect of soils from burned areas dominated by bracken and forest on the performance and traits of saplings from native tree species of Bolivia's tropical montane forest. In a controlled nursery experiment, we planted saplings from six species in three soil types: (a) soil from young sites (< 2 years since the last fire), (b) soil from old sites (> 8 years since the last fire), and (c) forest soil as control. We monitored growth, survival, chlorophyll content and functional traits for one year. Saplings developed higher growth rates in young than in old and forest soils, probably due to an increase in nutrients in young soils, which declines over time. Belowground biomass was lower in young soils compared to forest soils. Leaf production, chlorophyll content and leaf area were higher in burned than in forest soils, while other variables did not differ among soil types. Our results show that burned soils in bracken-dominated areas do not impair sapling development, suggesting that these soils do not negatively affect the performance of the species studied under controlled nursery conditions. Due to higher levels of nutrients in young soils, restoration strategies should focus on planting trees soon after fire.

Introduction

Tropical montane forests are among the most biodiverse ecosystems in the world and are characterized by high species richness and a high level of endemism in numerous taxonomic groups (Myers et al. 2000; Kessler 2002). However, large forested areas are highly degraded, commonly by fire events (Christmann et al. 2023), that frequently promote the development of *Pteridium esculentum* bracken ferns, hereafter bracken (Schneider and Fernando 2010; Velazco et al. 2024). Tropical forest regeneration in bracken-dominated areas is hindered (Marrs et al. 2000; Hartig and Beck 2003). However, the relative contribution of post-fire soil legacies to arrested forest regeneration remains poorly understood. Thus, identifying the factors that constrain forest regeneration under bracken dominance is essential to the development of restoration strategies.

Bracken is difficult to control due to its rapid growth and its persistent rhizome system, which enables rapid vegetative reproduction (Marrs et al. 2000). Its dominance can modify soil characteristics, leading to lower nitrogen, phosphorus, organic matter content, and pH in bracken burned areas than in forest soils (Snow and Marrs 1997; Valdez-Ramírez et al. 2020). On the other hand, other studies found higher concentrations of magnesium, calcium, potassium, and an increased nitrogen availability in bracken-dominated areas in comparison to the forest (Lippok et al. 2013). These changes in soil properties may affect sapling establishment and growth (Holste et al. 2011), suggesting that soil-mediated effects could contribute to reduced regeneration rates often observed in bracken-dominated areas.

Since bracken frequently establishes after fire, changes in soil properties may result from the combined effects of both bracken dominance and fire disturbance. Fire leads to physical, chemical and biological changes in soil properties (Agbeshie et al. 2022). It can alter soil physical structure by increasing erosion (Fachin and Thomaz 2025), and by enhancing soil hydrophobicity, which promotes greater surface runoff (Minervini et al. 2018). Suggesting that nutrient availability in burned bracken-dominated areas is dynamic and may depend on time since fire. For instance, nitrate and ammonium, the bioavailable forms of nitrogen, may initially increase after fire and then decrease within the following years (Jiang et al. 2022; Maidana-Tuco et al. 2025). Over longer periods, nutrient availability recovers due to microbial community regeneration, enhancing mineralization and nitrification, along with soil stabilization, improving nutrient and water retention (Verma et al. 2019). This temporal variation makes it important to compare saplings development in soils from recently and older burned bracken-dominated areas (hereafter soils from young sites and soils from old sites, respectively).

Tropical montane forest soils often show low and heterogeneous nutrient availability, particularly for nitrogen and phosphorus (Vitousek 1984). This condition is likely associated with high soil moisture and low temperatures, which reduce microbial mineralization of nitrogen and limit phosphorus availability (Dalling et al. 2016). Litterfall is a key pathway for nutrient cycling in tropical forests (Sayer et al. 2020). Therefore, deforestation and the slow litter decomposition in bracken-dominated areas may further reduce soil fertility by altering organic matter and nitrogen cycle processes (Ross 1993). Furthermore, the development of native species may be affected by fire legacies that alter soil nutrient dynamics.

Soil nutrient availability can alter functional traits and plant development (Minden and Venterink 2019). Under nutrient-poor conditions, plants may increase root exploration or belowground allocation to improve resource acquisition (Ushio et al. 2015; Ma et al. 2018). Leaf traits such as leaf area, specific leaf area and leaf dry-matter content may also shift along nutrient availability gradients, reflecting changes in resource acquisition and conservation (Schreeg et al. 2014; Cárate-Tandalla et al. 2018). However, it remains unclear how soils from burned bracken-dominated areas affect sapling growth, biomass allocation and leaf and root functional traits in tropical montane forest tree species.

The present study aims to answer the following questions: i) Do soils from forest and fire-deforested bracken-dominated areas affect the survival, growth and biomass of native tree saplings? ii) Does time since the last fire in bracken-dominated areas modify sapling performance? iii) Do leaf and root functional traits differ among saplings growing in soils from young sites, from old sites and from forest? We expect sapling performance (growth, survival, and biomass) to be higher in forests because post-fire environments often experience increased nutrient leaching and runoff (Minervini et al. 2018; Fachin and Thomaz 2025), which may reduce nutrient availability and negatively affect sapling performance. Given that phosphorus and nitrogen availability in soil increases in the first years after a fire and then declines over time (Jiang et al. 2022; Maidana-Tuco et al. 2025), we expect sapling performance to be higher in soils form young sites (< 2 years after fire) than in soils from old sites (> 8 years after fire). Finally, we expect that saplings will exhibit lower leaf area and specific leaf area, and higher root length in bracken

soils, as plants under nutrient poor conditions allocate more resources to roots to improve nutrient uptake (Lirio et al. 2019).

Methods

Study area

The study was conducted in municipality of Chulumani, Sud Yungas Province, department of La Paz, Bolivia (16°24'S, 67°31'W). The study area is on the eastern slopes of the Andes in the tropical montane humid forest, between 1,800 and 2,350 m a.s.l. The landscape consists of fragments of mature forest surrounded by large extensions of areas deforested by fire in different stages of succession, and coca (*Erythroxylum coca*) crops for traditional use (Lippok et al. 2013; Gallegos et al. 2016; Beck et al. 2024). Much of the deforested areas are dominated by the fern *Pteridium esculentum* and shrubs, or grasses in more degraded environments (Gallegos et al. 2016).

To establish the experiment, we took 0–20 cm depth soil samples from a total of 15 different sites within our study area from the following three types of environments. These soil types were: a) recently burned bracken-dominated areas, with less than two years since the last fire (soils from young sites; b) older burned bracken-dominated areas, with more than eight years since the last fire, (soils from old sites), and c) mature forest interior, hereafter forest soils. Soil samples collected from the experimental pots were combined and homogenized by soil type. Three mixed subsamples per soil type were subsequently sent to the Laboratorio de Ingeniería del Medio Ambiente & Soluciones (LIMASOL, Oruro, Bolivia) for analyses of pH, available phosphorus, percentage of total nitrogen, and percentage of organic matter (Table 1). The time since last burning was established based on local knowledge and satellite images. The experiment was installed in a tree nursery at the Santiago de Chirca Biological Station (SCBS; 16°23'48.38" S, 67°34'53.54" W, 2090 m asl).

Table 1
Soil nutrient characteristics in forest and burned soils: young= soils from young sites (< 2 years since last fire), old= soils from old sites (> 8 years since last fire) and forest= soils from the forest. Values are based on three analytical subsamples per composite soil type. Means ± SE are shown.

Soil properties	Soil from young site	Soil from old site	Forest soil
pH	4.8 ± 0	5.12 ± 0.02	5.6 ± 0.14
Organic matter (%)	23.74 ± 1.99	8.12 ± 1.13	11.17 ± 0.23
Nitrogen (%)	0.91 ± 0.01	0.49 ± 0.03	0.62 ± 0.05
Phosphorus (mg/kg)	32.53 ± 0.58	36.39 ± 0.42	36.06 ± 6.24

Species selection and sapling production

We selected six native tree species that occur in forest interiors or forest edges in the study area and have a wide range of functional traits: *Viburnum seemenii, Solanum sp., Alchornea triplinervia* var. *sabana*, *Piper boliviana, Cupania* sp. nov., and *Alchornea triplinervia* var. *boliviana*. In 2022, all seeds were collected from at least 10 individuals per species in our study area, from populations separated by at least 5 km. Seeds from different maternal individuals were pooled by species, sown in seedbeds immediately after collection at the SCBS and watered every other day. Saplings of approximately one year old were transplanted into individual plastic pots of 8 cm diameter x 18 cm height for the experiment, in September 2023. Species identifications were verified using reference material from the Herbario Nacional de Bolivia.

Experimental design

The six species were planted in the three types of soil: young, old, and forest soils. We replicated this design in 24 randomly arranged blocks at the SCBS tree nursery, covered with a 65% shade cloth. Each block contained one sapling of each species in each soil type, resulting in 18 pots per block. Eight blocks were covered with a single layer of bracken litter, eight blocks with two layers of bracken litter, and the remaining eight blocks were left without bracken litter, resulting in a total of 432 pots. These litter layers were applied to assess the effect of litter accumulation on sapling performance in a completely crossed design, but these results will be published elsewhere. All pots were watered three times per week. We monitored sapling growth and survival once every three months for one year. For the analyses presented here, we used final survival, final number of leaves and relative growth rate calculated from initial and final height measurements.

At the end of the experiment, we approximated the leaf chlorophyll content by measuring the SPAD value of the oldest healthy leaf of the plant (Damtew et al. 2024). The SPAD value is an indicator of chlorophyll content in a sample leaf, which is measured by the transmittance of red (650 nm) and infrared (940 nm) radiation (Uddling et al. 2007). For each individual, the relative growth rate (RGR) was calculated as the difference between the natural logarithm of the final height and the natural logarithm of the initial height, divided by the number of days elapsed between the first and last measurements.

Functional traits

At the end of the experiment, we collected one fully expanded healthy leaf from each surviving plants to obtain the following functional traits: leaf area (LA), specific leaf area (SLA), and leaf dry-matter content (LDMC) using standardized protocols (Pérez-Harguindeguy et al. 2016). We also collected randomly selected three saplings per species and soil type to measure root length, aboveground biomass and belowground biomass (Pérez-Harguindeguy et al. 2016).

Statistical analysis

Using generalized linear mixed-effect models with the *glmmTMB* package (Brooks et al. 2017), we assessed the effects of soil type (young soil, old soil, and forest soil) on the following response variables, separately: RGR, aboveground biomass, belowground biomass, number of leaves, chlorophyll content, survival, and functional traits (log transformed). Gaussian error distributions were used for RGR, chlorophyll content, and log-transformed continuous traits and biomass variables. For the number of leaves, we assumed a Poisson distribution, or a negative binomial distribution in case of overdispersion (Buckley 2015). To analyze sapling survival, we applied a binomial distribution. Soil types and bracken litter layers were considered as fixed effects. Bracken litter was included to control for its effect on the response variables, but their effects are analyzed elsewhere. In all models, we included blocks and species as random effects. Each model was validated by analyzing the residuals with the *DHARMa* package (Hartig 2022). Then, we selected the best model using the dredge function of the *MuMIn* package (Barton 2024) to evaluate the effect of soil type. Subsequently, we calculated *P* values from log-likelihood ratio tests (LRT), comparing the model that included soil type with a null model (without fixed effects) using the *Anova* function of the *car* package (Fox et al. 2024). We also calculated the marginal R-squared for each model using the function r.squaredGLMM of the *MuMIn* package (Barton 2024). We performed Tukey post-hoc comparisons and plotted the values predicted by the models using the *emmeans* package (Lenth et al. 2025). All analyses were performed in R version 4.4.1 (R Core Team 2024).

Results

We recorded 389 surviving saplings out of the 432 included in the experiment. A total of 144 saplings were planted in each soil type, of which 133 survived in young soil (92.4%), 130 in old soil (90.3%) and 125 in forest soil (86.8%).

Effects of soil type on sapling performance

Soil type significantly affected the relative growth rate (RGR) of the evaluated saplings. The RGR of saplings grown in young soil was 1.3 times higher than in old soil and 1.8 times higher than in forest soil (Fig. 1a). Additionally, RGR in old soils was 1.3 times higher than in forest soils (Fig. 1a, Tables S1, S2). Survival and aboveground biomass did not change significantly among soil types (Fig. 1b-c; Tables S1, S2). We found 1.2 times higher belowground biomass in the forest soil than in the young soil, while old soil did not differ from young soil or forest soil (Fig. 1d; Tables S1, S2).

Saplings produced 1.7 times more leaves in young soil and 1.8 times more leaves in old soil compared to forest soil (Fig. 1e; Tables S1, S2). Chlorophyll content was highest in saplings grown in old soil, intermediate in young soil, and lowest in forest soil (Fig. 1f; Tables S1, S2).

Effect of soil type on functional traits

Leaf area was 1.6 times higher in young soil and 1.4 times higher in old soil in comparison with forest soil (Fig. 2a; Tables S1, S2). Specific leaf area and leaf dry matter content did not differ depending on soil type (Fig. 2b-c; Tables S1, S2). Root length was 1.2 times greater in old soil than in young soil, but there was no difference between forest soil and burned soils (Fig. 2d; Tables S1, S2).

Discussion

We investigated the effect of young and old soils from bracken sites, as well as forest soils on the development and functional traits of six native Andean tree species. Sapling performance in terms of relative growth rate, leaf number and chlorophyll content was higher in both burned soils compared to the forest soil. However, belowground biomass was lower in young soil compared to forest soil, and no differences were detected between soil types in terms of survival and aboveground biomass. Young soils showed higher relative growth rates than old and forest soils, but this advantage was not consistent across all evaluated traits. Our results suggest that bracken soils do not have a negative effect on the performance or traits of the species studied, during their early life stages, at least under nursery conditions. Overall, our results suggest that recently burned soils may temporarily promote sapling growth, whereas this benefit may diminish in older soils. However, further studies are needed to explore the role of soil properties on forest regeneration in bracken areas in the long-term.

Sapling performance on burned and forest soils

Contrary to our expectation that forest soil would improve sapling performance because burned soils may suffer from erosion and nutrient leaching (Minervini et al. 2018), we found lower RGR, number of leaves and chlorophyll content in forest soil compared to both burned soils. Additionally, saplings developed more belowground biomass in forest soil than in young soil and sapling survival and aboveground biomass did not differ among soil types. The observed tendency for high nitrogen and organic matter percentages in young soils may partially explain these patterns (Lirio et al. 2019; Qi et al. 2019). As these soil properties did not differ between forest and old soil, other unmeasured factors could affect sapling performance. Our results suggest that bracken-dominated soils do not negatively affect the development of native tree species. Similar earlier studies in our study area found that bracken fronds and litter conditions do not restrict the recruitment of native seedlings (Gallegos et al. 2015, 2016; López et al. 2024). Besides, similar survival and aboveground biomass among soil types suggest that these variables are less influenced by soil characteristics and could be more sensitive to other factors such as herbivory (Fleury et al. 2015) or light conditions (Montgomery and Chadzon 2002).

In our study, the potential allelopathic effects of bracken soils were not strong enough to reduce sapling performance (De Jesus Jatoba et al. 2016). Previous studies found that bracken extracts inhibit seed germination and development of herbs (Mira et al. 2021), had species-specific effects on the development of juvenile native trees (Silva Matos and Belinato 2010), or weak negative effects on seed germination of native tree species (Maidana-Tuco et al. 2025). A possible explanation for our results could be the absence of a continuous supply of fresh bracken fronds during the experiment, which may

have reduced the accumulation of the potential allelochemicals in the soil (De Jesus Jatoba et al. 2016), reducing their effects on the saplings under study.

Sapling performance on young and old soils

In line with our second hypothesis, we found that the RGR of saplings was higher in young soil than in old soil. One explanation is the transient increase in nutrient availability following fire, which in our experiment tended to decline over time. However, the absence of changes in other parameters indicates that native saplings are able to develop despite changes in soil after fire. The higher RGR we observed in young soils compared with old soils is consistent with the results of Maidana-Tuco et al. (2025) for *Morella pubescens* and *Vismia plicatifolia*. This pattern may be explained by the higher nitrogen and organic matter content we observed in young soils compared with old soils. These observations contrast with the findings of Valdez-Ramirez et al. (2020), who found similar nutrient availability between young and old soils colonized by bracken (Valdez-Ramírez et al. 2020) but are consistent with other reports from bracken areas (Maidana-Tuco et al. 2025). Post-fire soil erosion in old soil may contribute to the apparent decline in the availability of nutrients, as vegetation removal and soil exposure after burning can increase runoff and exacerbate the loss of soil nutrients (Agbeshie et al. 2022; Fachin and Thomaz 2025). Therefore, restoration measures should prioritize young burned areas to utilize these transient nutrient pulses to promote the growth of native saplings.

Nevertheless, survival, aboveground biomass, belowground biomass and leaf number were not different between young and old soils. This suggests that, although the trend towards declining nutrients affects growth rates, the species studied are capable of maintaining stable development even under nutrient-poor conditions. These patterns may reflect the species adaptation to naturally nutrient-poor soils that are common in humid tropical forests (Amissah et al. 2026). Additionally, our results show an increase in chlorophyll content of saplings growing in old soil. This pattern contrasts with findings in other tropical trees, where nutrient availability is typically associated with an increase in chlorophyll production (Liu et al. 2024). Nonetheless, other studies suggest that plants in nutrient-poor soils can reallocate the nitrogen to leaves, or other photosynthetic structures, to preserve chlorophyll synthesis (Collins et al. 2022). However, we did not directly assess internal nutrient dynamics, and these questions should be addressed in future studies.

Effect of soil type on sapling functional traits

Contrary to our third hypothesis, LA was significantly larger in both burned soils than in forest soil. This pattern may be related to nutrient deficiency in forest soils, as such environments can lead to the formation of smaller leaves (Pérez-Harguindeguy et al. 2016; Bardy et al. 2023). In our experiment, forest soils tended to have lower levels of organic matter and nitrogen compared to young soil. However, SLA and LDMC did not change among soil types, suggesting that nutrient availability does not affect these traits, at least for the species studied. Our results suggest that functional traits do not depend solely on soil nutrient dynamics following fire, and that future studies should take into account other physical and chemical parameters that change in bracken-dominated environments.

The root length was significantly higher in old soil than in young soil and did not differ between forest and burned soils. A possible explanation could be that plants tend to allocate more root biomass when soil nutrients are limited (Poorter et al. 2012; Kramer-Walter and Laughlin 2017). Other factors also could explain the need to develop larger roots in old soil. For example, in humid tropical ecosystems native species commonly rely on strong associations with mycorrhizal and other microorganisms, which enhance nutrient uptake (Cardoso and Kuyper 2006; Reichert et al. 2022). The effect of fire and bracken dominance may alter biotic communities in the soil, influencing the efficiency of resource acquisition by plants. Consequently, plants may compensate by increasing the investment in root structures in old soil than in young soil (Poorter et al. 2012). Nevertheless, further studies are needed to understand all the factors that affect the development of root traits in fire deforested habitats.

Conclusions

Based on a controlled nursery experiment, our findings show that bracken soils do not negatively affect the early development of native tree species. The higher growth rates observed in young soil, likely due to nutrient releases following a fire, suggest that recently burned areas may offer a temporary opportunity for restoration measures. Nevertheless, factors such as herbivory, light availability, soil moisture, litter effects, competition and long-term survival can also influence the establishment of native species, thereby affecting forest regeneration. Our findings also highlight that the relationships between soil characteristics and functional traits in tropical montane ecosystems can be complex and are not always straightforward. The fact that leaf traits do not differ across soil types suggests that not all functional traits are equally sensitive to variation in soil nutrient availability, and points to a certain degree of resilience in native Andean montane species. The increase in root length in old soil, on the other hand, indicates a trade-off whereby plants under nutrient deficiency invest more in their root structures. As other factors, such as biological interactions, the physical properties of the soil, and the effect of litter on soil properties could affect sapling development, future studies should include controlled experiments to determine the importance of these factors.

Declarations

Acknowledgements

We thank Noel Taboada, Cecilia López and Cesar Mayta for help with the experiment setup and its maintenance. We also thank the Herbario Nacional de Bolivia and the Santiago de Chirca Biological Station for allowing us to use their facilities to work.

Funding

This study was funded by the German Research Foundation (DFG, grant He 3041/23–1) and by the Missouri Botanical Garden.

Data availability

Data will be available at Zenodo Repository

Author Contributions

Emili A. Jimenez: Writing – original draft, statistical analysis, investigation, data curation. **Daniela Ramos-Chuquimia**: Writing-review & editing, investigation, data curation. **Sara Morales:** Writing-review & editing, investigation, data curation. **Sebastian Tello:** Writing-review & editing, funding acquisition. **Carla Maldonado:** Writing-review & editing, validation, supervision. **Isabell Hensen:** Writing-review & editing, validation, funding acquisition. **Silvia C. Gallegos:** Writing-review & editing, validation, supervision, project administration, funding acquisition, data curation.

Competing Interests

The corresponding author confirms on behalf of all authors that there has been no involvement that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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Figures

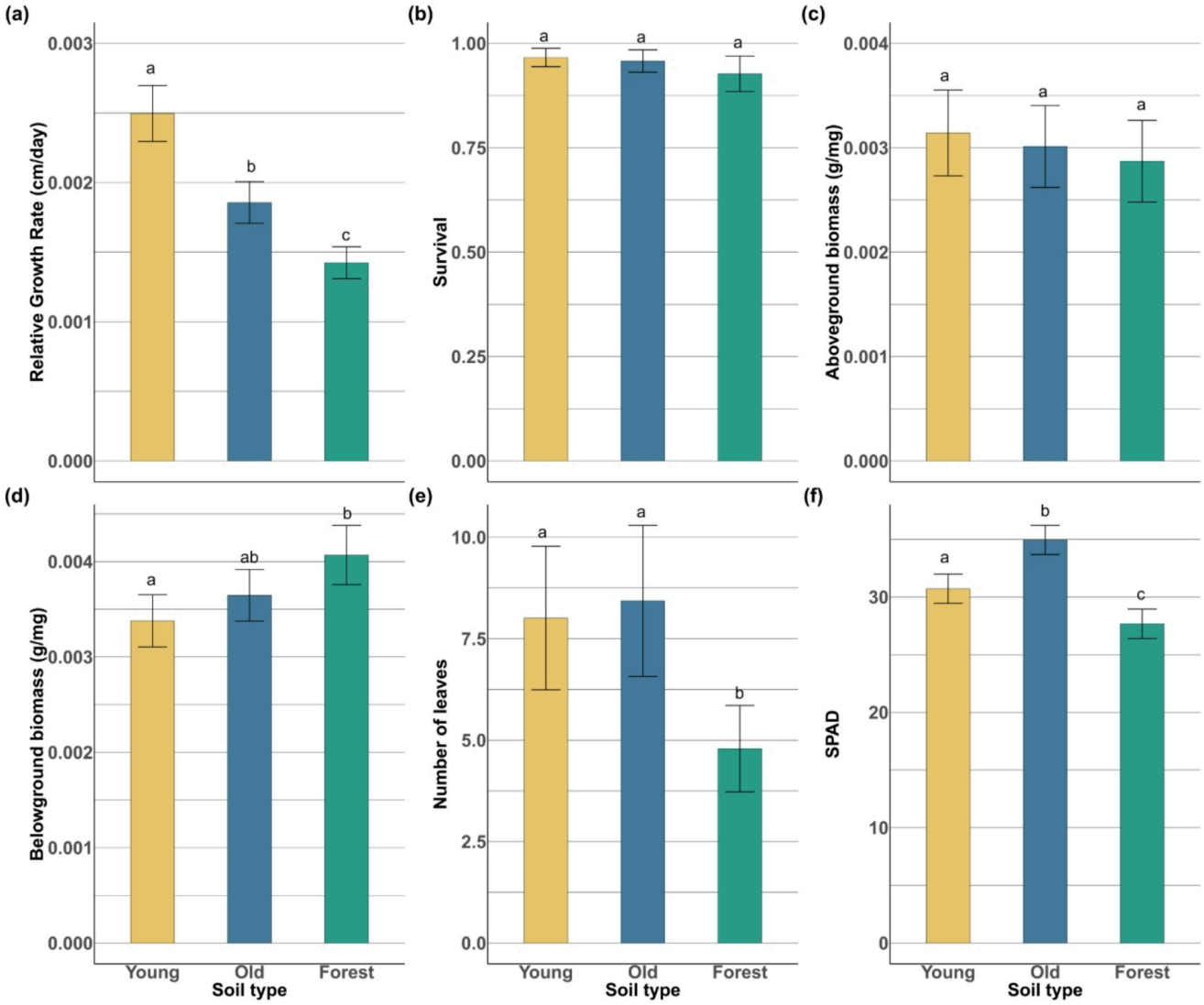


Figure 1

Effect of soil types: young= soils from young sites (< 2 years since last fire), old= soils from old sites (>8 years since last fire) and forest= soils from the forest interior as a control on seedling performance of six Andean montane forest species. Panels show responses in: (a) relative growth rate, (b) sapling survival, (c) aboveground biomass, (d) belowground biomass, (e) number of leaves, and (f) chlorophyll content as SPAD. Means ± SE are shown. Different lowercase letters indicate significant differences between soil treatments ($P < 0.05$).

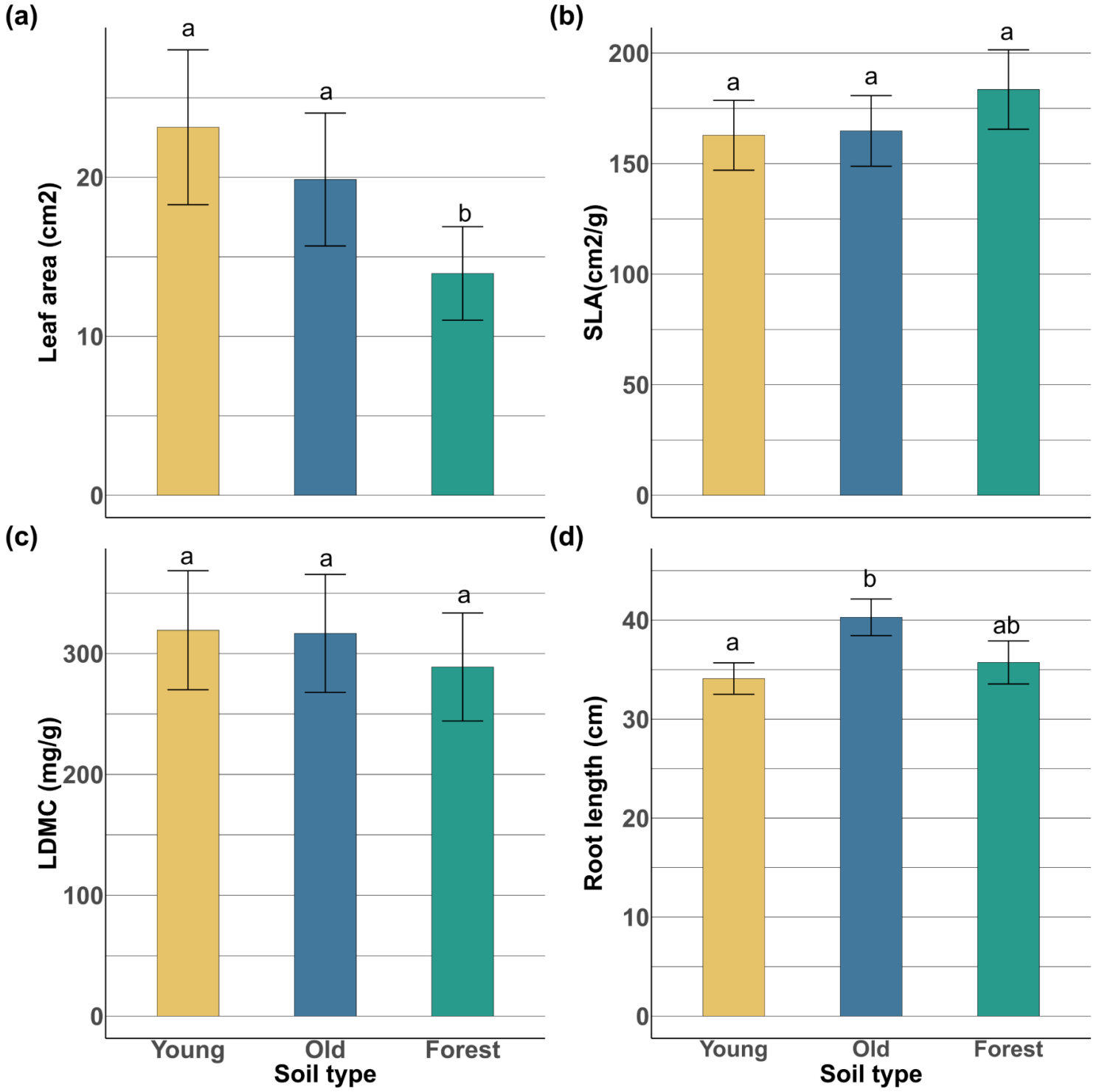


Figure 2

Effect of soil types: young= soils from young sites (< 2 years since last fire), old= soils from old sites (>8 years since last fire) and forest= soils from the forest interior as a control on sapling leaf and root traits of six Andean montane forest species. Panels show responses in: (a) leaf area, (b) specific leaf area, (d) leaf dry matter content, and (f) root length. Means ± SE are shown. Different lowercase letters indicate significant differences between soil treatments ($P < 0.05$).

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