The role of bracken’s fronds and litter on tree seedling performance in a tropical montane forest: a trait based approach

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Content

Summary

Tropical montane forests are among the most biodiverse ecosystems in the world. They harbor an extremely diverse and unique flora and fauna, with many species that only occur there. However, these forests are increasingly threatened, mainly due to anthropogenic disturbances such as land-use change and human-induced fire, which alter their composition and functionality. In particular, fire has become a recurrent disturbance, resulting in increasing deforestation and soil degradation. As a result of fires, bracken fern (*Pteridium* spp.) often dominates the vegetation for long periods. This highly competitive pioneer species thrives in disturbed environments, and natural forest succession is arrested. Seedling recruitment in bracken-dominated areas is typically constrained by a combination of abiotic filters (i.e., light availability, soil and air temperature, soil moisture) and biotic filters, including plant-plant interactions (facilitation/competition) and potential allelopathic effects. However, the role of bracken in forest succession is unclear, particularly whether it favors or competes with other species during the forest regeneration process. Furthermore, tree species are under strong seed dispersal limitation, resulting from a low abundance and differences in species composition of seed-dispersing animals. This leads to reduced tree recruitment and further delays forest regeneration. Therefore, active restoration is required to overcome dispersal limitation in these environments. Moreover, since not all tree species are able to develop in bracken presence, a trait-based approach could enhance the species selection in restoration programs.

This thesis consists of five studies that contribute to disentangle the role of bracken fronds and litter in early development of tree seedlings, with a particular focus on the functional traits that are favored to overcome environmental filters in fire-disturbed habitats. Through a series of experimental treatments involving the removal of bracken fronds and litter, I examined their facilitative or inhibitory effects on seedling establishment, recruitment, and growth. Additionally, I evaluated how plant functional traits influence species ability to persist in bracken-dominated areas. Finally, I compared the effectiveness of different restoration techniques and managing bracken strategies to guide restoration programs.

In Chapter II, I assessed the effects of bracken fronds and litter on the density and diversity of naturally recruited seedlings. My findings indicate that bracken presence supports a higher density and diversity of animal-dispersed tree species compared to treatments where fronds and litter were removed. Additionally, I found that environmental conditions shaped by bracken, such as light availability, soil temperature, and litter depth, influenced recruitment patterns, showing a positive relationship with abundance and species diversity of tree species, especially animal-dispersed, while I found a negative relationship with other life forms such as herbs and vines.

Chapter III focuses on the effect of bracken presence on the soil seed bank (SSB) in fire-deforested tropical montane areas. I found that tree and zoochorous species had significantly higher abundance and richness in the SSB of the forest than in bracken-dominated areas, indicating strong dispersal limitation. Within bracken treatments, species richness and diversity of SSB were highest in the presence of both fronds and litter, supporting that these components create favorable microclimatic conditions that maintain seed viability. The results of Chapters II and III showed similar patterns, suggesting that the arrested succession observed in these ecosystems is mainly driven by dispersal limitation. In both chapters, results suggest that bracken fronds and litter influence species composition by creating microclimatic conditions that affect seedling recruitment and seed viability. My findings highlight the need to assess the specific role of fronds and litter in facilitation and competition, as well as to investigate the traits that enable certain species to establish and grow in bracken-dominated environments. Thus, a trait-based approach is crucial for optimizing species selection in restoration efforts.

In Chapter IV, I explored how bracken fronds and litter differentially affect seedling establishment, recruitment success, and growth of 24 tree species in relation to seed size. I studied their effects based on direct seeding and transplanting field experiments over 36 months. I found that seedling establishment and recruitment success increased significantly with seed size, particularly in the presence of both fronds and litter. Additionally, I analyzed the direction and the intensity of these interactions classifying the set of species as small-, medium- and large-seeded species. My results showed that fronds generally facilitated seedling establishment, recruitment, and growth across all seed size categories, whereas litter accumulation negatively affected the establishment of small-seeded species. These findings highlight the need to consider both biotic and abiotic factors when designing effective restoration strategies in bracken-dominated areas.

In Chapter V, I explored which functional traits were favored by bracken presence in a seed addition experiment to guide species selection for active restoration in bracken-dominated areas. Furthermore, I explored if the species with the highest recruitment probabilities in bracken-dominated areas were abundant in old-growth forests. I identified eight functional traits that improve seedling performance under bracken, where bird-dispersal, large-seed size and traits related to shade-tolerance showed the greatest advantage. However, despite their ability to establish in bracken-dominated areas, the species with these traits were not among the most abundant species in old-growth forests.

My results suggest that abundant species in old-growth forests, which are commonly selected for planting in restoration programs, are not always the most suitable to recruit in bracken-dominated areas. Trait-based seed addition and seedling transplant experiments should be performed to guide species selection in restoration projects.

In Chapter VI, I compared the effectiveness of two restoration techniques: seed addition and seedling planting, under different bracken management treatments. Seedling planting resulted in higher recruitment success and growth than seed addition across all bracken treatments. However, seed addition reached nearly 50% of recruitment success when bracken fronds and litter were present, remaining as a promising restoration strategy, particularly for large-seeded animal-dispersed species, which have higher establishment probabilities in bracken-dominated areas as shown in Chapters IV and V. The complete removal of fronds and litter led to lower recruitment rates, reinforcing the role of bracken in mitigating harsh post-fire conditions. These findings suggest that integrating both restoration techniques, with a focus on stress-tolerant, large-seeded animal-dispersed species, could enhance forest recovery without requiring intensive bracken control.

Taken together, the results of all previous chapters of this thesis, provide experimental evidence on the complex interactions between bracken and tree species in fire-disturbed habitats. While bracken influences species recruitment by modifying abiotic conditions such as light availability and litter accumulation, it can also facilitate the establishment of mid- and late-successional species, particularly those with large seeds and dispersed by animals. Thus, given the high dispersal limitation, my results highlight the need for active restoration interventions. Although some studies suggest bracken removal, my results support maintaining bracken fronds and litter to take advantage of the microclimatic stability they provide. Direct seed addition and seedling planting of shade-tolerant species with traits such as large seed-size, thick bark, and high stem-specific density can enhance their recruitment. Additionally, prioritizing short-statured, animal-dispersed species, many of which are short-lived breeders with high recruitment rates, could accelerate natural regeneration by attracting seed dispersers and promoting seed rain. These actions may be even more effective when implemented soon after fire disturbances, before the accumulation of thick litter layers that further restricts seedling establishment of some species. However, as these results reflect only the early stages of seedling development, long-term studies are needed to assess their persistence and contribution to accelerate forest recovery.

Zusammenfassung

Tropische Bergwälder gehören zu den artenreichsten Ökosystemen der Welt. Sie beherbergen eine außergewöhnlich vielfältige und einzigartige Flora und Fauna, mit vielen Arten, die ausschließlich dort vorkommen. Diese Wälder sind jedoch zunehmend bedroht, hauptsächlich durch anthropogene Störungen wie Landnutzungsänderungen und vom Menschen verursachte Brände, die ihre Zusammensetzung und Funktionalität verändern. Insbesondere Feuer ist zu einer wiederkehrenden Störung geworden, die zu zunehmender Entwaldung und Bodendegradation führt. Als Folge von Bränden dominiert oft der Adlerfarn (*Pteridium* spp.) über lange Zeiträume die Vegetation. Diese hochkompetitive Pionierpflanze gedeiht in gestörten Umgebungen und blockiert die natürliche Waldsukzession. Die Rekrutierung von Baumkeimlingen in von Farn dominierten Gebieten wird typischerweise durch eine Kombination aus abiotischen Filtern (z. B. Lichtverfügbarkeit, Boden- und Lufttemperatur, Bodenfeuchtigkeit) und biotischen Filtern, einschließlich Pflanzeninteraktionen (Facilitation/Konkurrenz) sowie potenziellen allelopathischen Effekten, eingeschränkt. Die Rolle des Adlerfarns in der Waldsukzession ist jedoch unklar, insbesondere ob er die Regeneration anderer Arten fördert oder hemmt. Darüber hinaus unterliegen Baumarten einer starken Samenausbreitungsbegrenzung, die auf eine geringe Anzahl und veränderte Artenzusammensetzung der Samenverbreitenden Tiere zurückzuführen ist. Dies führt zu einer verringerten Baumrekrutierung und verzögert die Waldregeneration zusätzlich. Daher sind aktive Restaurierungsmaßnahmen erforderlich, um die Verbreitungsbegrenzung zu überwinden. Da nicht alle Baumarten in von Farn dominierten Gebieten gedeihen können, könnte ein merkmalsbasierter Ansatz die Artenauswahl in Restaurierungsprogrammen verbessern.

Diese Dissertation umfasst fünf Studien, die dazu beitragen, die Rolle von Farnwedeln und Farnstreu für die frühe Entwicklung von Baumkeimlingen zu entschlüsseln, mit besonderem Fokus auf funktionelle Merkmale, die das Überwinden von Umweltfiltern in feuerbeeinflussten Habitaten begünstigen. In einer Reihe experimenteller Behandlungen, bei denen Farnwedel und Streu entfernt wurden, untersuchte ich deren fördernde oder hemmende Effekte auf die Etablierung, Rekrutierung und das Wachstum von Keimlingen. Zusätzlich bewertete ich, wie pflanzliche funktionelle Merkmale die Fähigkeit von Arten beeinflussen, in von Farn dominierten Gebieten zu überleben. Schließlich verglich ich die Wirksamkeit verschiedener Restaurierungstechniken und Strategien zur Farnkontrolle, um Restaurierungsprogramme zu unterstützen.

In Kapitel II untersuchte ich die Auswirkungen von Farnwedeln und Streu auf die Dichte und Diversität natürlich rekrutierter Keimlinge. Meine Ergebnisse zeigen, dass die Anwesenheit von Farn eine höhere Dichte und Diversität tierverbreiteter Baumarten unterstützt als Behandlungen, bei denen Wedel und Streu entfernt wurden. Außerdem beeinflussten die durch den Farn geprägten Umweltbedingungen wie Lichtverfügbarkeit, Bodentemperatur und Streutiefen die Rekrutierungsmuster, wobei ein positiver Zusammenhang mit der Häufigkeit und Diversität von Baumarten bestand, insbesondere von tierverbreiteten Arten, während sich bei anderen Wuchsformen wie Kräutern und Lianen ein negativer Zusammenhang zeigte.

Kapitel III konzentriert sich auf die Auswirkungen der Farnpräsenz auf die Boden-Samenbank (SSB) in durch Feuer entwaldeten tropischen Berggebieten. Ich stellte fest, dass Bäume und zoochore Arten eine signifikant höhere Häufigkeit und Artenvielfalt in der SSB des Waldes als in von Farn dominierten Gebieten aufwiesen, was auf eine starke Verbreitungsbegrenzung hinweist. Innerhalb der Farnbehandlungen war der Artenreichtum und die Diversität der SSB am höchsten bei gleichzeitiger Anwesenheit von Wedeln und Streu, was unterstützt, dass diese Komponenten günstige Mikroklimabedingungen schaffen, die die Samenviabilität erhalten. Die Ergebnisse von Kapitel II und III zeigen ähnliche Muster und deuten darauf hin, dass die verzögerte Sukzession in diesen Ökosystemen hauptsächlich durch Verbreitungsbegrenzung bedingt ist.

In Kapitel IV untersuchte ich, wie Farnwedel und Streu die Etablierung, den Rekrutierungserfolg und das Wachstum von 24 Baumarten in Abhängigkeit von der Samengröße unterschiedlich beeinflussen. Über 36 Monate analysierte ich diese Effekte anhand von Freilandexperimenten mit Direktsaat und der Transplantation von Setzlingen. Ich stellte fest, dass der Erfolg von Etablierung und Rekrutierung signifikant mit der Zunahme der Samengröße anstieg, insbesondere in Anwesenheit von Farnwedeln und Laubstreu. Diese Ergebnisse unterstreichen die Notwendigkeit, biotische und abiotische Faktoren bei der Entwicklung wirksamer Restaurierungsstrategien zu berücksichtigen.

Im Kapitel V führte ich ein Experiment zur Direktsaat durch, um zu untersuchen, welche funktionellen Merkmale in von Farnen dominierten Gebieten begünstigt werden, mit dem Ziel, die Auswahl von Baumarten für die aktive Wiederherstellung zu optimieren. Ich identifizierte acht funktionelle Merkmale, die das Wachstum von Keimlingen unter Farnen fördern, wobei von Tieren verbreitete, großsamige und schattentolerante Arten die größten Vorteile zeigten. Allerdings waren diese Arten trotz ihrer Fähigkeit, sich in von Farnen dominierten Gebieten zu etablieren, in alten Wäldern nicht die häufigsten. Meine

Ergebnisse legen nahe, dass die in Wiederherstellungsprojekten häufig ausgewählten Baumarten nicht immer die am besten geeigneten für die Rekrutierung in Farnbeständen sind.

In Kapitel VI verglich ich die Wirksamkeit von zwei Restaurierungstechniken: Direktsaat und Setzlingspflanzung unter verschiedenen Farnmanagement-Strategien. Setzlingspflanzung führte in allen Behandlungen zu höheren Rekrutierungserfolgen und stärkerem Wachstum als Direktsaat. Jedoch erreichte die Direktsaat in der Präsenz von Farnwedeln und Streu fast 50 % Rekrutierungserfolg, was sie zu einer vielversprechenden Restaurierungsstrategie macht, insbesondere für großsamige, tierverbreitete Arten. Die vollständige Entfernung von Farnwedeln und Streu führte zu niedrigeren Rekrutierungsraten und unterstreicht die Rolle des Farns bei der Milderung extremer Umweltbedingungen nach Bränden.

Zusammenfassend liefern die Ergebnisse dieser Dissertation experimentelle Belege für die komplexen Wechselwirkungen zwischen Adlerfarn und Baumarten in feuerbeeinflussten Habitaten. Während Farn die Rekrutierung durch Modifikation abiotischer Bedingungen wie Lichtverfügbarkeit und Streuakkumulation beeinflusst, kann er auch die Etablierung von mittel- und spät-sukzessionalen Arten mit großen, tierverbreiteten Samen fördern. Angesichts der starken Verbreitungsbegrenzung unterstreichen meine Ergebnisse die Notwendigkeit aktiver Restaurierungsmaßnahmen. Trotz Vorschlägen zur Farnentfernung zeigen meine Ergebnisse, dass das Belassen von Farnwedeln und Streu vorteilhaft sein kann. Direktsaat und Setzlingspflanzung schattentoleranter Arten mit Merkmalen wie großer Samengröße, dicker Rinde und hoher Holzdichte könnten ihre Rekrutierung verbessern. Zudem könnte die Priorisierung von kleinwüchsigen, tierverbreiteten Arten die natürliche Regeneration durch die Anziehung von Samenverbreitern beschleunigen. Da diese Studien nur frühe Keimlingsstadien betrachten, sind Langzeitstudien erforderlich, um ihren Beitrag zur Waldregeneration zu bewerten.

Resumen

Los bosques montanos tropicales se encuentran entre los ecosistemas más biodiversos del mundo. Albergan una flora y fauna extremadamente diversa y única, con muchas especies que solo se encuentran allí. Sin embargo, estos bosques están cada vez más amenazados, principalmente debido a perturbaciones antropogénicas como el cambio en el uso del suelo y los incendios provocados por el ser humano, que alteran su composición y funcionalidad. En particular, el fuego se ha convertido en una perturbación frecuente, lo que resulta en una creciente deforestación y degradación del suelo. Como consecuencia de los incendios, el helecho (*Pteridium* spp.) suele dominar la vegetación durante largos períodos. Esta especie pionera altamente competitiva prospera en ambientes perturbados y donde la sucesión natural del bosque es lenta. El reclutamiento de plántulas en áreas dominadas por el helecho suele estar limitado por una combinación de filtros abióticos (como la disponibilidad de luz, la temperatura del suelo y del aire, y la humedad del suelo) y filtros bióticos, incluyendo las interacciones planta-planta (facilitación/competencia) y posibles efectos alelopáticos. Sin embargo, el papel del helecho en la sucesión no está claro, en particular si favorece o compite con otras especies durante el proceso de regeneración del bosque. Además, las especies arbóreas enfrentan una fuerte limitación en la dispersión de semillas debido a la baja abundancia y diferencias en la composición de especies de animales dispersores, lo que reduce el reclutamiento de árboles y retrasa aún más la regeneración del bosque. Por lo tanto, se requiere restauración activa para superar esta limitación de dispersión en estos ambientes. Además, dado que no todas las especies arbóreas pueden desarrollarse en presencia del helecho, un enfoque basado en rasgos funcionales podría mejorar la selección de especies en los programas de restauración.

Esta tesis consiste en cinco estudios que contribuyen a entender el papel de las frondas y la hojarasca de *Pteridium* en el desarrollo temprano de plántulas de árboles, con un enfoque particular en los rasgos funcionales que les permiten superar los filtros ambientales en hábitats afectados por incendios. A través de una serie de tratamientos experimentales que implicaron la eliminación de frondas y hojarasca del helecho, evalué sus efectos facilitadores o inhibitorios sobre el establecimiento, reclutamiento y crecimiento de plántulas. Además, evalué cómo los rasgos funcionales de las plantas influyen en la capacidad de las especies para persistir en áreas dominadas por el helecho. Finalmente, comparé la efectividad de diferentes técnicas de restauración y estrategias de manejo del helecho para orientar programas de restauración.

En el Capítulo II, evalué los efectos de las frondas y hojarasca de *Pteridium* sobre la densidad y diversidad de plántulas reclutadas naturalmente. Mis hallazgos indican que la presencia del helecho promueve una mayor densidad y diversidad de especies arbóreas reclutadas naturalmente, principalmente aquellas dispersadas por animales en comparación con los tratamientos donde se eliminaron las frondas y la hojarasca. Además, encontré que las condiciones ambientales modificadas por el helecho, como la disponibilidad de luz, la temperatura del suelo y la profundidad de la hojarasca, influenciaron los patrones de reclutamiento, mostrando una relación positiva con la abundancia y diversidad de especies arbóreas, especialmente las dispersadas por animales, mientras que encontré una relación negativa con otras formas de vida, como hierbas y enredaderas.

El Capítulo III se centra en el efecto de la presencia del helecho sobre el banco de semillas del suelo (SSB, por sus siglas en inglés) en áreas tropicales montanas deforestadas por incendios. Encontré que las especies arbóreas y zoócoras tenían una abundancia y riqueza significativamente mayores en el SSB del bosque que en las áreas dominadas por *Pteridium*, lo que indica una fuerte limitación en la dispersión. Dentro de los tratamientos con frondas y hojarasca, la riqueza y diversidad de especies en el SSB fueron mayores, lo que sugiere que estos componentes crean condiciones microclimáticas favorables que mantienen la viabilidad de las semillas. Los resultados de los Capítulos II y III mostraron patrones similares, sugiriendo que la lenta sucesión en estos ecosistemas se debe principalmente a la limitación en la dispersión. En ambos capítulos, los resultados sugieren que las frondas y la hojarasca de *Pteridium* influyen en la composición de especies al modificar condiciones microclimáticas que afectan el reclutamiento de plántulas y la viabilidad de semillas.

En el Capítulo IV, exploré cómo las frondas y la hojarasca de *Pteridium* afectan diferencialmente el establecimiento, el éxito de reclutamiento y el crecimiento de plántulas de 24 especies arbóreas en relación al tamaño de semilla. Estudié estos efectos mediante experimentos de siembra directa y trasplante de plántulas en el campo durante 36 meses. Encontré que el establecimiento y el éxito de reclutamiento de plántulas aumentaron significativamente con el tamaño de la semilla, particularmente en presencia de frondas y hojarasca. Además, analicé la dirección e intensidad de estas interacciones clasificando las especies en pequeñas, medianas y grandes semillas.

En el Capítulo V, en un experimento de adición de semillas, exploré qué rasgos funcionales fueron favorecidos para sobrepasar los filtros en ambientes dominados por *Pteridium* para guiar la selección de especies en la restauración activa. Identifiqué ocho rasgos funcionales que mejoran el desempeño de las plántulas en presencia del helecho, destacándose la dispersión por aves, el gran tamaño de semilla y los rasgos relacionados con la tolerancia a la sombra. Sin embargo, a pesar de su capacidad para establecerse en áreas dominadas por el helecho, las especies con estos rasgos no fueron las más abundantes en los bosques maduros.

En el Capítulo VI, comparé la efectividad de dos técnicas de restauración: la adición de semillas y la siembra de plántulas, bajo diferentes tratamientos de manejo del helecho. La siembra de plántulas resultó en un mayor éxito de reclutamiento y crecimiento que la adición de semillas en todos los tratamientos. Sin embargo, la adición de semillas alcanzó casi un 50 % de éxito de reclutamiento cuando las frondas y la hojarasca estaban presentes, lo que la convierte en una estrategia prometedora, particularmente para especies dispersadas por animales y de semillas grandes, que tienen mayores probabilidades de establecimiento en áreas dominadas por el helecho.

En conjunto, los resultados de esta tesis proporcionan evidencia experimental sobre las complejas interacciones entre el helecho y las especies arbóreas en hábitats afectados por incendios. Aunque el helecho modifica las condiciones abióticas como la disponibilidad de luz y la acumulación de hojarasca, también puede facilitar el establecimiento de especies de sucesión media y tardía, especialmente aquellas con semillas grandes dispersadas por animales. Dado que la limitación en la dispersión es alta, mis resultados resaltan la necesidad de intervenciones de restauración activa. A pesar de que algunos estudios sugieren la eliminación del helecho, mis hallazgos apoyan el mantenimiento de sus frondas y hojarasca para aprovechar la estabilidad microclimática que brindan. La adición de semillas y la siembra de plántulas de especies tolerantes a la sombra con rasgos como semillas grandes, corteza gruesa y alta densidad del tallo pueden mejorar su reclutamiento. Sin embargo, dado que estos resultados reflejan solo las etapas iniciales del desarrollo de plántulas, se requieren estudios a largo plazo para evaluar su persistencia y contribución a la recuperación del bosque.

Chaper I. General introduction

Introduction

Tropical montane forests are among the most biodiverse ecosystems in the world (Myers et al., 2000), harboring approximately 50% of the world's species, including a high proportion of endemics (Rahbek et al., 2019; Pillay et al., 2022), these forests play a crucial role in global biodiversity conservation, not only as reservoirs of species richness but also as key contributors to ecological processes such as carbon storage, nutrient cycling, and water regulation (Paulick et al., 2017). However, they are increasingly threatened due to human disturbances such as land-use change and deliberate fires (Kessler and Beck, 2001; Oliveras et al., 2018). In the last decades, fire has become a recurrent disturbance, leading to extensive deforested and degraded areas (Laurance et al., 2012; Aguilar-Garavito et al., 2021), promoting fire-adapted vegetation (Asbjornsen and Wickel, 2009). In these environments, highly dominant species can establish, with ferns of the genus *Pteridium* being of particular concern due to their ability to persist through recurrent fires (Stewart et al., 2008).

The genus *Pteridium* (hereafter referred to as bracken) is the most widely distributed Pteridophyte, occurring in all continents except Antarctica, and often dominating the vegetation for long periods (Marrs et al., 2000; Marrs and Watt, 2006; Amouzgar et al., 2023), arresting forest succession (Hartig and Beck, 2003; Christmann et al., 2023). Bracken ferns are highly competitive pioneer species that thrive in disturbed environments (Roos et al., 2010) and maintain their dominance through multiple mechanisms that hinder the establishment of other plant species (Marrs et al., 2000). Their dense frond canopy creates heavy shading (Hartig and Beck, 2003; Silva Matos and Belinato, 2010), while the deep litter layer from decomposing fronds potentially acts as a physical barrier that influences seed bank germination and seedling establishment (Ghorbani et al., 2006). Additionally, bracken possesses a highly persistent rhizome system and produces potential allelopathic compounds that may further inhibit plant growth (Marrs et al., 2013; De Jesus Jatoba et al., 2016). These competitive characteristics contribute to reduce tree and shrub species richness as bracken coverage increases (Günter et al., 2007; Paz et al., 2022).

Despite its long-term dominance, the role of bracken in tropical forest regeneration remains controversial. Some studies suggest that bracken inhibits forest regeneration due to the dense cover of its fronds and litter, which limit light availability for other plants (Myster et al., 2022; Paz et al., 2022). In contrast, other studies found that tree seedling survival and growth rates in bracken-dominated areas are comparable to those in forests (Gallegos et al., 2016). Bracken can mitigate temperature and water stress in adult plants

(Paz et al., 2022). Tree seedling performance tends to be higher in bracken-dominated areas than in areas where bracken has been removed, both for naturally regenerating seedlings and those established through seed addition (Gallegos et al., 2015, 2016). Similar patterns have been observed in South America and Africa (Silva Matos and Belinato, 2010; Palomeque et al., 2017; Ssali et al., 2017, 2018). The low recruitment of tree species may be attributed to dispersal or establishment limitations (Münzbergová and Herben, 2005). Dispersal limitation occurs when the arrival of seeds to a given site is restricted due to limited seed production, ineffective dispersal mechanisms, or the absence of dispersal agents (Nathan and Muller-Landau, 2000; Münzbergová and Herben, 2005). In bracken-dominated areas, it is primarily associated with the scarcity of natural perches and food resources for birds, the main seed dispersers in these environments (Saavedra et al., 2015). Establishment limitation occurs when seed germination, seedling survival, or growth are hindered by biotic or abiotic factors (Muller-Landau et al., 2002; Münzbergová and Herben, 2005). Species differ in their ability to overcome establishment limitation, depending on their functional traits and tolerance to environmental stressors. While some species may persist or establish successfully under bracken cover (de Souza Carvalho et al., 2016; Ssali et al., 2017), the specific traits that allow species to outcompete bracken and promote successional transitions remain poorly understood. Bracken not only creates a dense frond and litter layer that shade other plants, but also produces secondary metabolites that may have allelopathic effects (Marrs and Watt, 2006; Jatoba, 2023), further limiting the recruitment of tree species. However, other studies suggest that its allelopathic effects on tree species are weak (Maidana-Tuco et al., 2025). Understanding which species can tolerate or overcome these conditions and which traits are associated with these abilities is crucial for guiding evidence-based restoration efforts.

Plants can be classified as early-, mid- and late-successional species according to their abundance at each successional stage, which is determined by its physiological characteristics such as shade-tolerance (Bazzaz, 1979). Previous studies have suggested that factors such as light availability (Ssali et al., 2019) and soil properties (Lippok et al., 2013; Valdez-Ramírez et al., 2020) influence succession in bracken-dominated areas, with late-successional species showing better performance under bracken (Günter et al., 2009; Silva Matos and Belinato, 2010). However, the role of bracken fronds and litter, as separate components in shaping these dynamics, remains unclear. This distinction is critical because, while bracken litter has been reported to limit seed bank germination and impede natural recruitment in temperate regions (Ghorbani et al., 2006), other studies in tropical ecosystems suggest that bracken fronds may facilitate seedling germination and survival (Gallegos et al., 2015, 2016; Ssali et al., 2019). Since most tropical tree species rely on animal dispersal and do not form persistent seed banks (Wijdeven and Kuzee, 2000; Palma et al., 2021), understanding whether bracken fronds and litter function as a barrier or a facilitator for the soil seed bank and seedling recruitment is essential for guiding restoration strategies.

Since bracken is considered a difficult plant to control (Marrs et al., 1998; Le Duc et al., 2000), two management strategies are commonly used to reduce bracken cover: (i) chemical control, which includes the application of herbicides such as asulam or glyphosate (Hallam et al., 1987; Dolling, 1996) and (ii) mechanical control, which consist in physical damage to the fronds or rhizome commonly through the use of heavy machinery (Ghorbani et al., 2006) or manually clearing by machete (Douterlungne et al., 2013). Although bracken often recovers rapidly (Marrs et al., 1998), the continuous cutting controlled bracken effectively in temperate regions (Cox et al., 2007; Stewart et al., 2008). In contrast to the temperate region, in the tropics, climatic conditions allow bracken fronds to regrow year-round (Roos et al., 2010) and *Pteridium* species are shade-intolerant (Xavier et al., 2019), suggesting the need of different strategies. Some studies in the tropics recommend planting fast-growing native trees combined with frequent mechanical removal of bracken fronds to accelerate forest recovery while suppressing bracken growth through shading and competition (Douterlungne et al., 2013; Aguilar-Dorantes et al., 2014). However, maintaining repeated cutting of fronds is costly (Xavier et al., 2023). Therefore, determining the most effective management strategy requires a better understanding of the ecology of bracken-dominated areas in tropical environments.

Consequently, restoration techniques such as seed addition and seedling planting offer promising solutions for enhancing plant density and diversity (Slocum et al., 2006; Douterlungne et al., 2010; Palomeque et al., 2017; Toledo-Aceves et al., 2022) and to overcome dispersal limitation. Seed addition increases the availability of propagules at sites where natural seed rain is scarce, while seedling planting reduces mortality in early-stages and improves recruitment success (Khurana and Singh, 2001; Holl and Aide, 2011). However, their effectiveness remains context-dependent, as bracken-dominated areas impose multiple abiotic (e.g., light availability, temperature, humidity) and biotic (e.g., competition, allelopathy) filters that can hinder seedling establishment.

In this context, identifying species capable of overcoming bracken-related constraints requires a trait-based approach. Functional traits serve as indicators of ecological strategies (Wright et al., 2007; Visser et al., 2016), also influence key ecological processes, revealing trade-offs that shape plant survival and growth (Díaz et al., 2004), and can help predict species’ responses to environmental limitations (Metz et al., 2023).

For example, seed size is a critical determinant of recruitment success, as larger seeds generally provide greater energy reserves that enhance seedling establishment under stressful conditions (Moles and Westoby, 2006). Leaf traits such as leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC) are linked to resource-use strategies: species with high SLA tend to maximize light capture and rapid growth, whereas those with high LDMC are associated with stress tolerance and conservative resource use (Wright et al., 2004; Reich, 2014). Other traits such as wood density and tree height are key structural traits influencing demographic rates and species' performance under stressful conditions. Wood density is often associated with a trade-off between growth rate and survival, where species with high wood density invest in mechanical resistance and drought tolerance but exhibit slower growth (Iida et al., 2014).

By integrating these functional traits into species selection, restoration efforts can improve predictions of establishment success under the challenging conditions imposed by bracken. Short-term screening of growth and survival rates may further refine this selection, ensuring the resilience of planted species in degraded ecosystems (Martínez-Garza et al., 2013). This approach can also be applied to restoration programs in other regions with different species pools, broadening its ecological relevance and scalability.

Thesis objectives

The aim of my thesis was to understand the role of bracken fronds and litter in seedling performance. Additionally, I aimed to identify the functional traits favored by bracken. To address these objectives, my thesis comprises five experimental studies (Chapters II-VI). I established experimental bracken management plots with different combinations of frond and litter removal treatments. In these plots, I collected data on natural seedling recruitment and the soil seed bank. I also compared the performance of tree species under different restoration techniques including direct seed addition and the transplant of nursery-raised seedlings. Furthermore, I obtained functional trait data from each species to analyze which traits are favored in bracken-dominated areas.

In Chapter II, I analyzed the effect of bracken fronds and litter on the natural recruitment of plants from different life forms, successional stages, and dispersal syndromes. I also examined how species richness and abundance varied in response to environmental variables across treatments.

In Chapter III, I assessed the effect of bracken fronds and litter on the abundance, richness, and diversity of emerged seedlings from the soil seed bank. For these analyses I classified the seedlings based on their life form and dispersal syndrome.

In Chapter IV, by using seed addition and seedling planting experiments within the bracken management treatments, I examined the direction (i.e., facilitation or competition) and intensity of interactions between bracken fronds/litter and tree seedlings, considering seed size as a key factor on this interaction.

In Chapter V, based on the seed addition experiment and functional trait analyses from adult trees, I identified the functional traits that enhance the establishment success of tree seedlings under bracken presence. Moreover, I explored if the species with these traits are common in secondary forests.

In Chapter VI, I compared the effectiveness of two different restoration techniques and evaluated the impact of bracken management on tree species recruitment and growth. This analysis provided insights into the most effective planting strategy and *Pteridium* management approach to optimize forest restoration in bracken-dominated areas.

In Chapter VII, I synthesize the key findings, explore their implications for forest regeneration and for effective restoration strategies, and offer perspectives for future research directions.

Chapter II. Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-disturbed tropical montane habitats

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Abstract

Tropical montane forests are diverse ecosystems often affected by uncontrolled human-induced fires causing tree mortality and creating large deforested areas. After fires, *Pteridium* spp. ferns (bracken) often dominate, and forest regeneration in these areas is slow. In this study, we evaluated the effects of bracken fronds and litter, as well as the micro-environmental conditions created by the fern, on the density and species diversity of naturally recruiting seedlings. At eight sites, 120 experimental plots were established among forest and bracken-dominated areas with the following treatments: (a) fronds and litter intact (F+L+); (b) fronds intact and litter removed (F+L-); (c) fronds removed and litter intact (F-L+); and (d) fronds and litter removed (F-L-). After one year all seedlings were registered, identified and classified according to their life-form (tree, shrub, herb, vine), dispersal vector (wind- or animal-dispersed) and successional status (early-, mid-, and late-successional). For all treatments we assessed 13 micro-environmental variables. We identified 3,649 naturally-recruiting seedlings corresponding to 278 species from 70 families. We found positive effects of bracken fronds particularly on tree seedling recruitment: The density of animal- and wind-dispersed tree seedlings were 2.1 and 6.1 fold higher in treatments with fronds than without fronds, respectively. Similarly, the diversity of animal-dispersed, mid- and late-successional tree species was 2.8, 1.9 and 4.3 times higher in the treatments with fronds. The environmental conditions generated by bracken, such as photosynthetically active radiation, live bracken biomass and litter depth, had positive effects on the recruitment of seedlings of mid- and late-successional, and animal-dispersed tree species, and negative effects on seedlings of other life-forms, notably early successional species. To promote forest regeneration in bracken-dominated areas, active ecological restoration measures such as direct seed addition and transplants of nursery-raised seedlings of mid- and late-successional species should be considered. As bracken can hinder the establishment of some species but favor others, it is recommended to include a trait-based approach to understand species responses to environmental factors and select species that are optimally adapted to bracken-dominated habitat conditions.

Keywords: Arrested succession, dispersal syndrome, habitat recovery, *Pteridium*, successional status, tree recruitment.

1. Introduction

Tropical montane forests are exposed to a variety of threats that are primarily attributable to human activities (Gardner et al., 2009; Laurance et al., 2012). Agricultural expansion through slash-and burn and uncontrolled fires has led to extensive fire-disturbed areas (Gardner et al., 2009; Laurance et al., 2012). After fire, ferns of the genus *Pteridium* (hereafter referred as bracken) rapidly dominate the landscape for a long time (Carvalho et al., 2022; Hartig & Beck, 2003). Bracken is widespread worldwide (Marrs et al., 2000) and is generally difficult to control (Stewart et al., 2008).

In tropical fire-disturbed areas dominated by bracken, forest regeneration is slow (Hartig & Beck, 2003; Palomeque et al., 2017), and is related to the fern's resilience and success as a competitive species (Roos et al., 2010). Bracken's success is mainly attributed to its dense fronds and deep litter accumulation, which shades other species and prevents their establishment (Marrs et al., 2000), and to allelopathic effects that affect the growth and development of particular seedling species (Jatoba, 2023; Silva Matos & Belinato, 2010). This suggests establishment limitation (i.e. failure in seed germination, seedling survival and/or growth due to biotic or abiotic factors) (Muller-Landau et al., 2002; Münzbergová & Herben, 2005). Alternatively, slow forest regeneration in bracken-dominated areas may also be linked to dispersal limitation (i.e., a failure of seeds to reach a site, Gallegos et al., 2016), which may be related to the lack of natural perches and food sources for birds, which are the main seed dispersers in these areas (Saavedra et al., 2015).

To reduce establishment limitation, some experimental efforts in temperate and tropical climates have tried to reduce bracken's dominance and biomass by cutting and using herbicides (Milligan et al., 2016; Pakeman et al., 2002; Xavier et al., 2023).The most effective strategies for reducing bracken density in the tropics consisted of cutting bracken fronds every 2-4 weeks and planting fast-growing pioneer trees or shrubs by seed broadcasting, direct sowing or nursery-raised-seedling transplants (Douterlungne et al., 2010, 2013; Toledo-Aceves et al., 2022; Vleut et al., 2013). However, maintaining repeated cutting of fronds is costly (Aguilar-Dorantes et al., 2014; Xavier et al., 2023). Additionally, other factors such as the incorporation of mid- and late-successional animal-dispersed species should be considered to ensure forest succession (Levy-Tacher et al., 2015). Determining the most effective management strategy requires a better understanding of the ecology of bracken-dominated areas in tropical environments.

In bracken-dominated areas, factors such as light availability (Ssali et al., 2019) and soil properties (Lippok et al., 2013; Valdez-Ramírez et al., 2020) can influence forest succession (Guariguata & Ostertag, 2001). Considering the abundance of a species at each successional stage, which is determined by its physiological characteristics such as shade-tolerance, plants can be classified as early-, mid- and late-successional species (Bazzaz, 1979). The direction and speed of succession in secondary tropical forests depends mainly on the arrival and establishment of seeds (de la Peña-Domene & Martínez-Garza, 2018), because most species do not form a seed bank (Palma et al., 2021; Wijdeven & Kuzee, 2000). Given the unfavorable conditions in most deforested tropical areas, many forest species have limited ability to establish (de la Peña-Domene & Martínez-Garza, 2018; Martínez-Ramos et al., 2016). Surprisingly, Gallegos et al. (2016) found high seedling survival and growth of tree and non-tree species in bracken-dominated areas, and bracken fronds were found to increase seed germination, seedling growth and survival of late-successional tropical species (Gallegos et al., 2015, 2016; Ssali et al., 2019), suggesting little establishment limitation. Nevertheless, bracken litter can form a physical barrier reducing seed bank germination, preventing seeds from reaching the ground, and inhibiting natural recruitment in temperate zones (Ghorbani et al., 2006). However, the role of bracken fronds and litter have not been disentangled in tropical ecosystems, and their effects should be assessed to improve our understanding of forest regeneration processes in fire-disturbed tropical montane forests. Furthermore, an analysis of environmental conditions could help to understand the specific effects of bracken fronds and litter on the seedling community.

We conducted an experimental study to gain a better understanding of the effects of traditional management strategies for bracken control on natural seedling recruitment and the specific micro-environmental conditions that allow seedling recruitment of different species in tropical bracken-dominated areas. We addressed the following questions: (i) What are the effects of bracken fronds and litter on density, species richness and diversity of naturally recruiting seedlings? We expected higher seedling recruitment of mid- to late-successional species with bracken fronds and litter than early-successional species, due to their higher shade-tolerance (Gallegos, 2015; Ssali et al., 2019). Additionally, given the dispersal limitation and the lack of perches in bracken-dominated areas (Gallegos et al., 2016; Saavedra et al., 2015), we also expected recruitment of animal-dispersed species to be lower in bracken than in forest, but higher in treatments with fronds and litter than in their absence. (ii) How do the micro-environmental conditions generated by bracken affect density and species richness of naturally recruiting seedlings? We expected; that increasing shade and soil moisture generated by bracken will negatively affect the density and richness of early-successional seedlings, whereas mid- and late-successional species would benefit from these micro-environmental conditions (Gallegos et al., 2016; Ssali et al., 2019).

2. Materials and methods

2.1. Study area

The study was conducted in the vicinity of Chulumani, province Sud Yungas, La Paz, Bolivia (16º24’37” S, 67º31’37” W), in a tropical montane forest located on the eastern slope of the Andes, between 1900 and 2400 m asl. The mean annual temperature is 20.5°C and the mean annual precipitation is about 1390 mm (Molina-Carpio et al., 2019). The forests in this area have become highly fragmented as a direct consequence of uncontrolled and frequent anthropogenic fires (Killeen et al., 2005) and agricultural expansion of Erythroxylum coca for traditional use (Killeen et al., 2008). The landscape consists of two large remnants of continuous old forests, of approximately 1500 and 3000 ha, surrounded by vast areas dominated by bracken fern (*Pteridium esculentum* subsp. arachnoideum (Kaulf.) J. A. Thomson) (Schwartsburd et al., 2018), wind-dispersed shrubs of Asteraceae and Melastomataceae, and some bird-dispersed species of Ericaceae (Lippok et al., 2013). At the forest edges, the most common tree species are *Hedyosmum racemosum* (Chlorantaceae), *Clusia elongata* (Clusiaceae) and *Hieronyma fendleri* (Phyllantaceae); while, species from the Rubiaceae, Piperaceae, Melastomataceae and Lauraceae families are abundant in the forest interior (see Lippok et al., 2014). Most woody species are dispersed by birds and bats (Lippok et al., 2014; 2013), although terrestrial mammals such as Mazama americana and Dasyprocta variegata can also disperse seeds (Gallegos et al., 2024).

2.2. Experimental design

At eight sites, each separated by at least 1 km, 50 x 50 m plots were established in bracken-dominated areas, at 100 m from the forest edge. The bracken-dominated areas were last burned 5-15 years before the start of the experiment and have since been dominated by bracken and a few scattered shrubs. To assess the effect of bracken fronds and litter on natural seedling recruitment, each plot was divided in four subplots of 25 x 25 m, with the following treatments: (a) with fronds and with litter (F+L+); (b) with fronds, without litter (F+L-); (c) without fronds, with litter (F-L+) and (d) without fronds, without litter (F-L-) (Fig. 1). To maintain these treatments, fronds were cut carefully with a machete at ground level and litter was removed manually every four months, during one year. Within each of the four subplots, three 1 m2 plots were randomly created to assess seedling density and species richness (Fig. 1). To provide a reference for seedling recruitment in the forest interior, we also established three 1 m2 plots in the forest interior of each site. In order to have similar conditions at the beginning of the experiment, we removed seedlings and saplings from all the 1 m2.

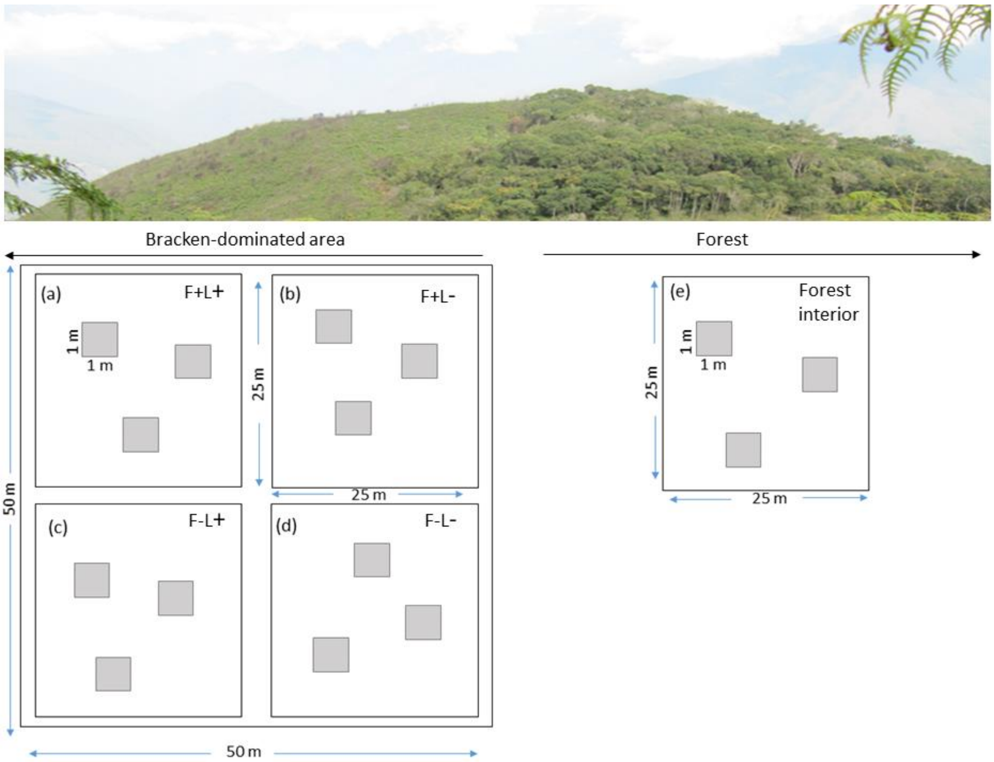

Fig.1. Details of the experimental design. Left: Arrangement of experimental subplots for treatments (25 x 25 m) and plots for natural recruitment (1 x 1 m) in the bracken-dominated areas: were (F+) represent bracken fronds presence, (F-) bracken fronds removal, (L+) bracken litter presence, and (L-) bracken litter removal. Right: plots for natural recruitment (1 x 1 m) in the forest interior.

2.2.1. Seedling sampling

One year after the establishment of the experiment, all seedlings above 2 cm height were measured and recorded in each plot. Similar seedlings for each morphospecies per site were collected out of the plots and compared. Saplings and adults near our plots were also collected for reference. All vouchers were dried and taken to the Herbario Nacional de Bolivia (LPB) for identification. We also used a seedling reference collection of more than 100 species sown in the tree nursery of the Santiago de Chirca Biological Station deposited at the LPB. After seedling comparison and identification, all species were classified according to their life-form (tree, shrub, herb or vine), dispersal vector (wind- or animal-dispersed) and successional status (early-, mid- and late-successional), according to the abundance of each species in plots established at different successional stages in previous studies (Gallegos et al., 2016; Lippok et al., 2014; Lippok et al., 2013), and based on expert knowledge, personal observations, and information at the LPB (Table S1).

2.2.2. Environmental factors

We measured environmental factors once during both the wet and dry seasons. We collected two soil samples in each subplot using a metal ring 3.5 cm in diameter and 5 cm in height. The soil samples were stored in hermetic bags to obtain their wet weight and then dried to obtain the dry weight and calculate soil moisture and soil bulk density (ISRIC 2002). Additional soil composite samples of each subplot were sent to the "Laboratorio de Calidad Ambiental" at the Universidad Mayor de San Andres (La Paz, Bolivia), for analyses of soil pH, exchangeable potassium, available phosphorus, soil organic matter, carbon and total nitrogen, following the ISRIC 4, ISRIC 9, ISRIC 14-3, ISRIC 5, ISRIC 5 and ISRIC 6 methods, respectively. The soil temperature was measured at three random points per subplot with a soil thermometer (ScienceFirst, Florida, USA). At five points per subplot we also measured the photosynthetically active radiation (PAR) with a PAR quantum sensor (Delta Ohm, Padova, Italy) connected to a photoradiometer (HD2102.2). For calibration, a reference data point was taken at 2 m height, pointing to a clearing (2m-PAR). Subsequently, PAR data were taken at 20 cm from the ground (20cm-PAR). To assess the relative PAR available for seedlings, we calculated DeltaPAR as (20cm-PAR/2m-PAR) x 100 (Gallegos et al., 2015). Litter depth was measured at the end of the study using a metal ruler from the ground to the top of the litter in at least three points of each 1 m2 plot where litter was present. Since the above-ground biomass consisted mostly of living and dead bracken fronds, we established two additional 1 m2 plots in each subplot where we collected all the above-ground bracken biomass, and then separated the living and dead fronds, which were dried and weighed separately.

2.3. Data analysis

To characterize the species diversity, we calculated the Hill numbers (q0= Species richness, q1= Shannon diversity and q2= Simpson diversity) (Chao et al., 2014), using the iNEXT package (Hsieh et al., 2016). We assessed the effect of bracken fronds and litter on seedling density and species diversity among treatments using generalized linear mixed-effects models (GLMM). We calculated the mean density and species diversity of the three 1 m2 plots in each subplot, and included seedling density and species diversity of the following life-forms as response variables in separate models: total, animal-, wind-dispersed, and early-, mid-, and late-successional trees, shrubs, herbs and vines (vines and lianas were pooled). In all models, we included treatment (F+L+, F+L-, F-L+, F-L-) as the fixed effect, and site as the random effect. Post hoc comparisons among treatments were performed in the emmeans package. The seedlings recruiting in the forest were not included in the models, and were only used as a reference in figures.

We used GLMMs to test the effect of environmental variables (soil pH, potassium, phosphorus, nitrogen, carbon, organic matter, soil bulk density, soil temperature, soil moisture, litter depth, dead- and live-bracken biomass and photosynthetically active radiation) on the same density and species richness (q0) response variables, with site as the random effect. All uncorrelated environmental variables were included as fixed effects in a full model and then we selected the best model with the lowest Akaike Information Criterion (AICc) with the MuMin package (Barton, 2018) and performed Likelihood Ratio Tests (LRT) to compare each best model with the null model. All models were performed with the glmmTMB package (Brooks et al., 2017). All statistical analyses were performed in R v.4.2.1 (R Core Team, 2022).

3. Results

3.1. Seedling recruitment

In the 120 plots established in the forests and bracken-dominated areas, we found a total of 3,649 naturally recruited seedlings from 278 morphospecies and 70 families. Most morphospecies (75.55%) were identified at the species level, 16.9% at the genus level, 7.55% at the family level, and 3.6% were not identified and were discarded from all analyses. A comparison of the seedlings registered in forests and bracken-dominated areas, according to their life-form, successional status and dispersal vector is shown in Table S2.

The most common tree species that recruited naturally in the forest were *Nectandra cuspidata*, *N. acutifolia* (Lauraceae) and *Clusia elongata* (Clusiaceae), and in the bracken-dominated areas were *Clethra scabra* (Clethraceae), *Myrsine coriacea* (Primulaceae) and *Weinmannia sorbifolia* (Cunoniaceae) (Table S1).

3.2. Effects of fronds and litter removal on natural seedling recruitment

The density and diversity of tree seedlings in the treatment with fronds and litter (F+L+) were 3.3 and 2.1 times higher than without fronds and without litter (F-L-) (Fig. 2a-d). The same pattern was observed for animal- and wind-dispersed tree species (Fig. 2e-l). Seedling density and diversity of shrubs and vines were not affected by bracken treatments (Fig. 2). Seedling density and richness of herbs were highest in the treatment with fronds and without litter (F+L-) than the other treatments (Fig. 2a-d).

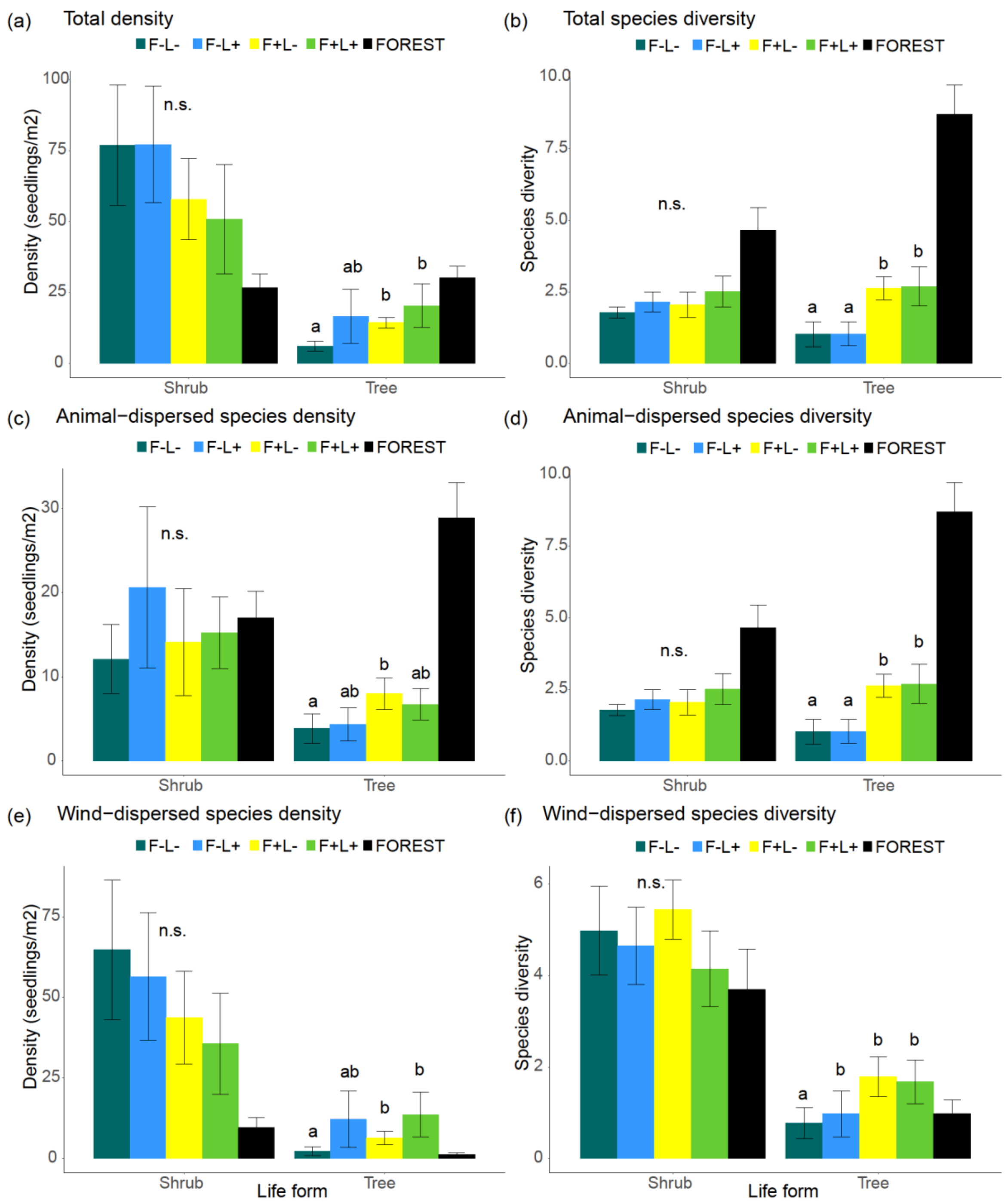

Fig. 2. Density (left panels) and species diversity of (a-d) total, (e-h) animal-dispersed, and (i-l) wind-dispersed naturally recruiting seedlings under different bracken treatments: with bracken fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Species diversity is expressed in terms of Hill numbers (Q0= Species richness, Q1= Shannon diversity and Q2= Simpson diversity). Different letters denote significant differences among treatments ($p < 0.05$). Shown are means ± SE. NA denotes that a statistical comparison was not feasible.

3.3 Successional status

Regarding successional status, the treatments with fronds (F+L+/F+L-) had higher density and species diversity of early, mid and late-successional tree species than F-L-. We did not register significant differences among treatments for vines, in any successional status. The comparison of total density of vines, herbs and shrubs from mid-successional status was not possible due to low data among treatments. As for species diversity herbs of mid-successional species had higher values of Shanon-Wiener and Simpson indices in F+L- compared to the other treatments (Figure 3 Table S4). Late successional shrubs had higher values of Shannon index in F+L+ compared to F-L- (Figure 3i. Table S4). Late-successional vine species had considerably higher density in F+L+ compared to F+L- and F-L+ (Figure 3i, TableS4).

3.4 Effects of micro-environmental conditions created by bracken on natural recruitment

The natural recruitment of tree seedlings in bracken-dominated areas was related to several environmental variables. We found a negative relationship between photosynthetically active radiation (PAR) and total, animal- and wind-dispersed, mid- and late-successional tree species in terms of density and diversity (Fig. 4, Table S3). The density of wind-dispersed species was related to an increase in soil bulk density. The density of mid- and late-successional tree species decreased with soil temperature. Seedling density of late-successional trees increased with higher biomass of living bracken, and their richness decreased with soil temperature (Fig. 4, Table S3). We found that total, animal-dispersed, mid- and late-successional tree species richness decreased with increasing PAR, and richness of late-successional species decreased with increasing soil temperature (Fig.4, Table S3).

Seedling density and richness of wind-dispersed and early-successional shrub species increased with soil bulk density and decreased with litter depth (Fig. S1, Table S4). Animal-dispersed shrubs’ density increased with PAR and their diversity decreased with soil temperature.

Seedling density of herbs decreased with litter depth and increased with soil moisture (Table S5). We did not find any effect of environmental variables on vine seedling density or species richness (Table S6). Differences of micro-environmental variables among treatments are in Table S7.

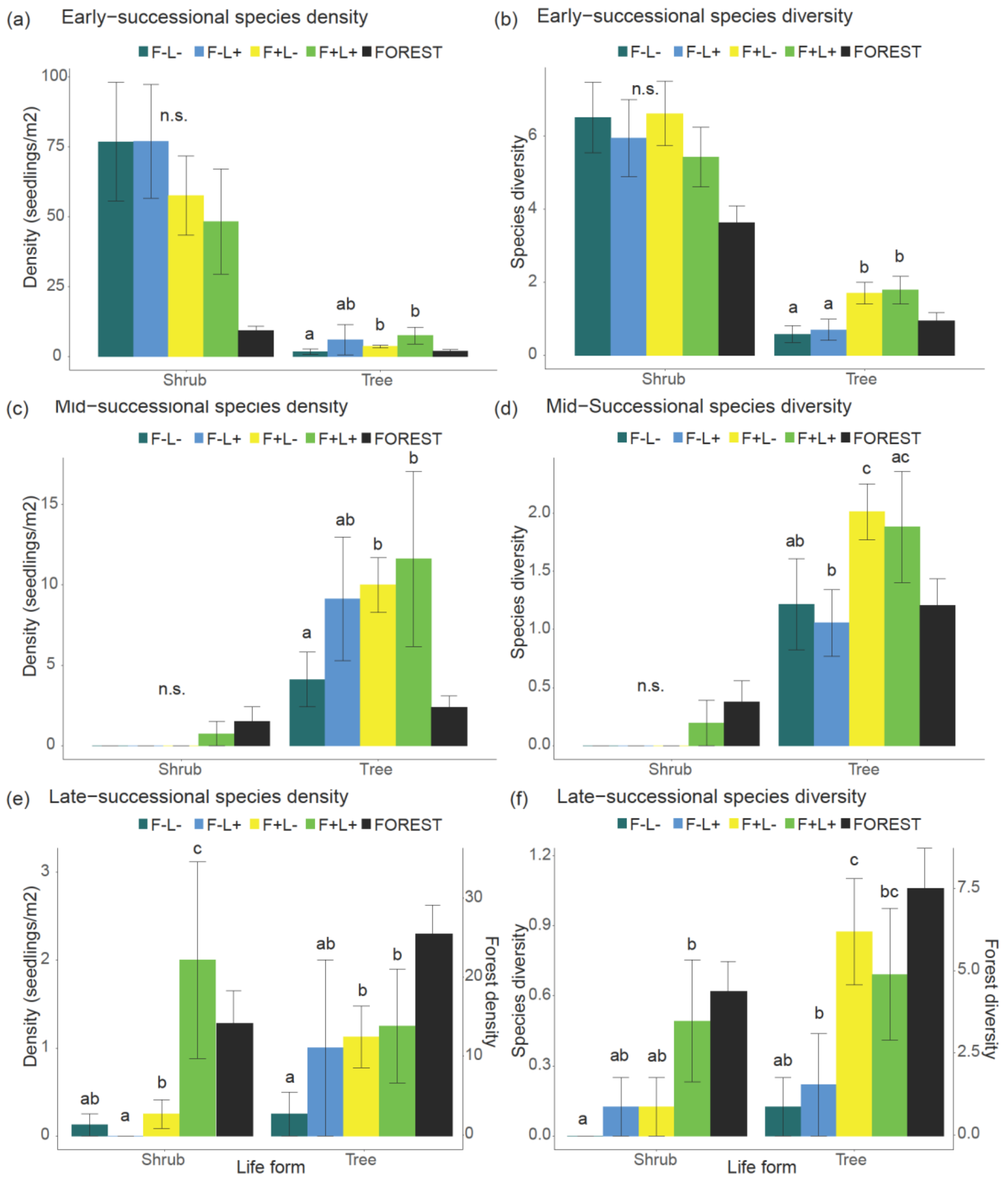

Fig. 3. Density (left panels) (a,e,i), and species diversity (q0) of: Early-, (b-e), mid-(f-h)-, and late-successional (j-i) naturally recruiting seedlings under different bracken treatments: with bracken fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Species diversity is expressed in terms of Hill numbers (Q0= Species richness, Q1= Shannon diversity and Q2= Simpson diversity). Different letters denote significant differences among treatments ($p < 0.05$). Shown are means ± SE. NA denotes that a statistical comparison was not feasible

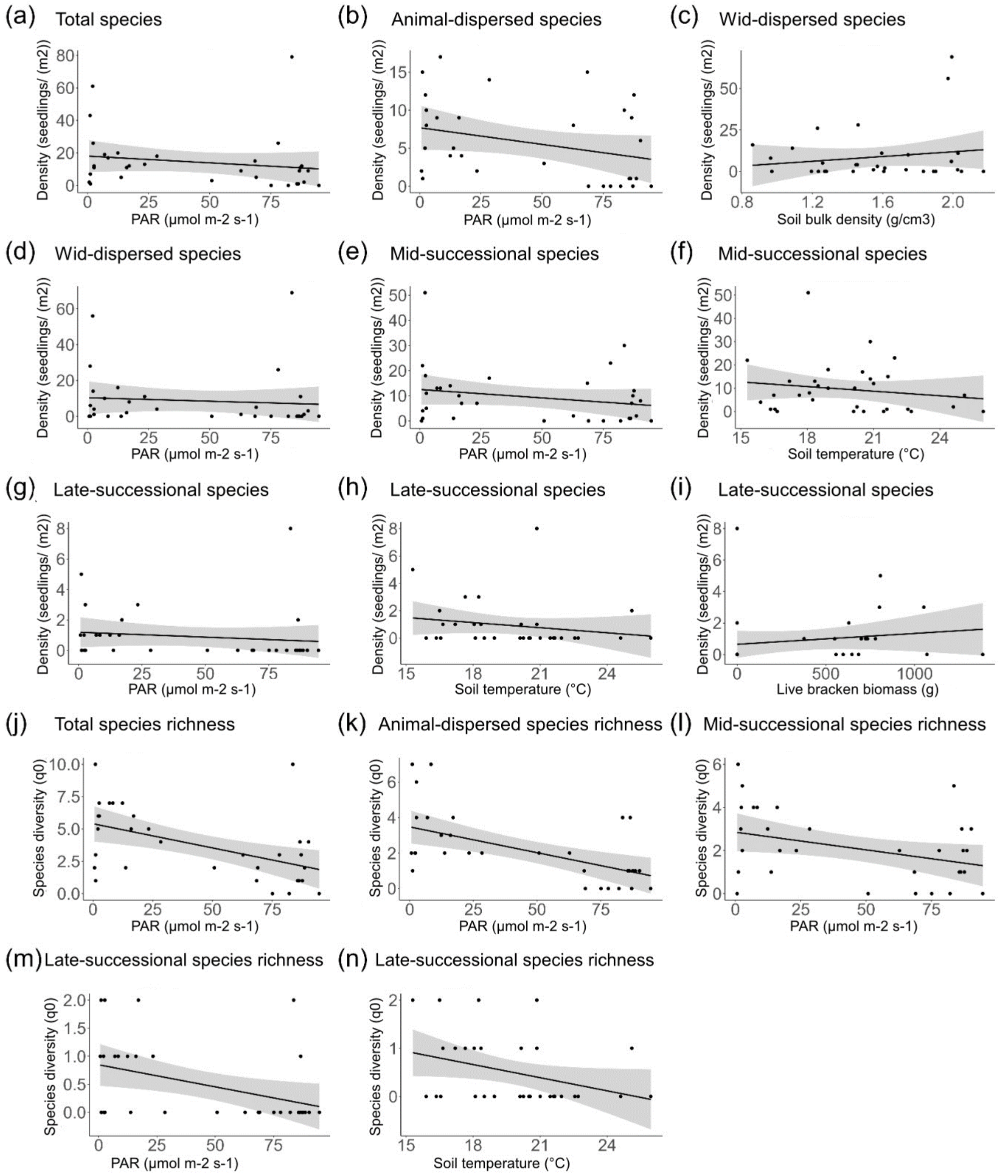

Fig. 4. Significant relationships between environmental variables and seedling density (a-i) and species richness (j-n) of tree species All variables were measured at the seedling survey units. The shaded area represents the 95% confidence interval. Only variables with statistically significant relationships ($p<0.05$) are shown.

4. Discussion

Our results show positive effects of bracken fronds and litter on the seedling density and species diversity of wind- and animal-dispersed, and mid- and late-successional tree species. On the other hand, removal of bracken fronds and litter had negative effects on natural recruitment of tree seedlings, and positive effects on wind-dispersed herb species. The positive effect of bracken on tree seedling density and diversity was related to environmental conditions. Bracken fronds' shading was positively related with the recruitment of mid- to late- successional and animal-dispersed tree species. In contrast, the density of wind-dispersed and early-successional shrubs and herbs were negatively affected by environmental conditions generated by bracken, such as litter depth. Given the favorable micro-environmental conditions created by bracken for animal-dispersed as well as for mid- and late-successional tree species, the inclusion of trees from these categories in active restoration strategies would be promising to promote forest regeneration.

4.1 Effects of fronds and litter on seedling recruitment

Although several studies suggest that bracken fronds could shade and inhibit establishment and recruitment of other species (Humphrey and Swaine, 1997; Marrs et al., 2000a; Paz et al., 2022), and that litter acts as a physical barrier that prevents the arrival of seeds to the ground inhibiting natural recruitment (Ghorbani et al., 2006; Pakeman and Hay, 1996), we found that seedling density and species richness of naturally recruiting mid- and late-successional tree species were higher under bracken fronds and litter than after their removal. These results are consistent with previous studies in the Neotropics (Gallegos et al., 2016, 2015) and in the Afrotropics (Ssali et al., 2019), suggesting that bracken is a potential facilitator for shade-tolerant and late-successional tree species. Thus, in contrast to other studies that found bracken to have a negative effect on seedling establishment (Carvalho et al., 2022; Paz et al., 2022), our experimental results show that bracken creates the environmental conditions necessary for the establishment of shade-tolerant and late-successional seedlings, and reduces harsh conditions of open areas.

With respect to bracken litter, previous studies have reported that litter accumulation acts as a barrier and prevents seed germination of herbs, grasses and shrubs in temperate zones (Amouzgar et al., 2020; Ghorbani et al., 2006). Our results are consistent with this pattern showing that seedling density and diversity of early-successional and wind-dispersed species of herbs and shrubs decrease with increasing litter depth, while tree seedlings were not affected by litter depth. Given that bracken litter biomass almost doubles in volume within one year (Rivas-Alonso et al., 2021), our results may be related to the fact that litter accumulation modifies environmental conditions, such as shading, moisture retention and temperature maintenance, which could either improve or hinder seedling establishment depending on their specific requirements (Jessen et al., 2023; Ssali et al., 2019).

Shading by bracken fronds could improve recruitment of shade-tolerant species, but early-successional species are hindered by bracken (de Souza Carvalho et al., 2016).

Therefore, our results support that bracken acts as an ecological filter mainly mediated by shading, as previously suggested by Ssali et al. (2019). The low seedling recruitment of early-successional species in bracken-dominated areas could be related to their light requirements, life-form and dispersal syndrome. Early-successional species in general require high light conditions for germination and growth (Everham et al., 1996), but depending on their life-form, non-tree species may have different filters and lower establishment probabilities (Garcia et al., 2016, 2015). Although some species of Melastomataceae and Asteraceae can persist on the soil seed bank in bracken-dominated areas (Xavier et al., 2016), previous studies found that the species richness and density in the soil seed bank is low (Lippok, Walter, et al., 2013; Ssali et al., 2018), and that seedling density and species richness is not associated with the seed bank but is associated to the seed rain (Gallegos et al. 2016, Ssali et al. 2018). Early-successional species tend to have smaller seeds than mid- or late-successional species (De La Peña-Domene et al., 2016; Rivas-Alonso et al., 2021), and their germination rates are higher only under high-light conditions (Pearson et al., 2002). Moreover, smaller seeds exhibit reduced competition during establishment and lower seedling vigour than larger seeds, which generally have greater resources to support seedling development (Murali, 1997; Westoby et al., 1996).

Although wind-dispersed seeds are able to move long distances in open areas, animal-dispersed seeds reach open areas only when their dispersal agents are present (Pearson et al., 2002; Rivas-Alonso et al., 2021). For bracken-dominated areas, Saavedra et al., 2015 reported severe seed limitation, mainly due to the lack of perching structures for birds, resulting in poor arrival of animal-dispersed seeds, especially for large-seeded and late-successional species. Most animal-dispersed seeds from the forest interior do not arrive in open areas until their dispersal agents find perches, shelter or food (Estrada and Coates-Estrada, 2005). In our study, *Miconia* (Melastomataceae) species were frequent in bracken-dominated areas. We found the highest abundance of *M. hygrophila* and *M. theazans*, both classified as mid-successional species, in the treatment with bracken fronds and litter. *Miconia* species are considered keystone plant resources for frugivorous birds and are the most species-rich zoochorous genus with long fruiting periods (Blendinger et al., 2011; Maruyama et al., 2013). Therefore, including *Miconia* and other animal-dispersed species in restoration strategies could foster the arrival of seed-dispersing birds to the bracken-dominated area. This strategy could help to reduce the differences in species composition of seed-dispersing birds and bats between the forest and bracken-dominated areas, pointed as one of the main causes of dispersal limitation (Gallegos et al., 2024).

4.2 *Effects of micro-environmental conditions on seedling recruitment*

Micro-environmental conditions determine the success of seed germination and seedling establishment (Eriksson and Ehrlén, 1992; Münzbergová and Herben, 2005). We did not find differences in soil nutrients among treatments. This could be related to the short duration of the experiment, which may not have been sufficient to produce differences in nutrients among treatments and to show differences in seedling density and species richness in relation to soil properties.

Soil compaction increases bulk density and reduces porosity (Beylich et al., 2010), and could have negative effects on the establishment of tree species (Corrià-Ainslie et al., 2015). In our study, treatments with bracken fronds had low bulk density and higher tree seedling density compared to treatments where bracken fronds were removed. Soils with higher bulk density could reduce water uptake and aeration, which in turn reduces seed germination, prevents root development, and causes higher tree seedling mortality (Hattori et al., 2013; Osuji, 1990). In open environments, the bulk density of the soil tends to be higher than in shaded environments (Gaitán et al., 2016), probably because the leaves can reduce soil erosion and compaction. For shrub species, we found an opposite pattern: density and species richness were positively correlated with bulk density. This pattern may be related to the capacity of non-tree species to colonize sites with degraded soils, which generally have higher bulk density (Islam et al., 2001).

Our treatments with bracken fronds and litter maintained soil moisture and likely reduced tree seedling mortality. Contrarily, the treatments without fronds and without litter had low tree seedling density and species richness, probably due to the low humidity and higher temperatures in open areas causing seedling mortality due to desiccation (Alvarez-Aquino et al., 2004; Khurana and Singh, 2001).

Plant species vary in their light requirements to germinate, establish, and grow (Montgomery and Chazdon, 2002; Yu et al., 2008). In our study, lower levels of photosynthetically active radiation were associated with higher tree density and species richness, suggesting that tree species tolerate shade under a bracken canopy and their recruitment could be improved by bracken fronds. Although few of the seedlings recorded in the bracken-dominated areas corresponded to late-successional species, we found evidence that bracken allows their recruitment and their low density is likely related to dispersal limitation (Gallegos et al., 2016). Most of the tree species surveyed belonged to the mid-successional group, which can grow under low or high light levels (Zhou et al., 2023), indicating their potential to become established, and to promote forest regeneration by providing food sources and perching structures for birds.

5 Implications for management

The succession of montane forests in bracken-dominated areas is frequently disrupted and remains arrested (Christmann et al., 2023). Our results highlight the importance of the micro-environmental conditions generated by bracken for natural recruitment of mid- and late-successional tree species, as well as for animal-dispersed tree species. Therefore, to promote forest regeneration in bracken-dominated areas, active ecological restoration strategies such as direct seed addition, and transplants of nursery-raised seedlings of mid- and late-successional species should be considered. If seedlings are transplanted from the nursery and the bracken fronds are not cut, a significant amount of combustible material remains, posing a fire risk. Therefore, seedlings should be transplanted soon after a fire to promote forest regeneration from the beginning and to take advantage of the amelioration in environmental conditions provided by bracken fronds after the fire. These strategies must be accompanied by a socialization of fire management in local communities, as they are key to restoration programs. Furthermore, our results highlight that dispersal limitation could be the main factor hindering forest regeneration, so the inclusion of attractants for seed dispersers should be evaluated.

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Chapter III. Influence of *Pteridium* fronds and leaf litter management on the soil seed bank characteristics in a fire-disturbed tropical montane forest

This chapter is under review in *Biotropica* as

Jiménez, E. A., **López, C. L.**, Fuentes, A. F., Hensen, I. & Gallegos, S. C. Influence of *Pteridium* fronds and leaf litter management on the soil seed bank characteristics in a fire-disturbed tropical montane forest

ABSTRACT

The bracken fern *Pteridium* spp. dominates the post-fire vegetation over long periods of time and affects the natural regeneration of the tropical montane forest. In bracken-dominated areas, arrival of animal-dispersed seeds is hindered due to dispersal limitation. Additionally, bracken fronds and litter can prevent seedling establishment and slow down forest regeneration. We investigated the effects of fronds and litter of *Pteridium* on the abundance, richness and diversity of the soil seed bank (SSB) in a tropical montane fire-deforested area in Bolivia. At eight study sites, located between 1,800 and 2,350 m.a.s.l, we collected soil samples in plots with different management treatments to control the tropical fern species *Pteridium esculentum* subsp*. arachnoideum* (bracken). SSB samples were collected from the following treatments: (a) with fronds and litter (F+L+), (b) with fronds and without litter (F+L-), (c) without fronds and with litter (F-L+), (d) without fronds and without litter (F-L-), and (e) forest. Using the seedling emergence method, SSB was assessed every 20 days over an eight-month period. The abundance and richness of tree and zoochorous species were significantly higher in the forest than in the bracken treatment. Among the bracken treatments, the species richness and diversity of tree and zoochorous species were highest in the treatment with bracken fronds and litter, while the lowest values were found in their absence. Our findings suggest that bracken fronds and litter lead to favorable microclimatic conditions that maintain the viability of these species in the SSB.

Keywords: bracken, forest restoration, natural regeneration, seed dormancy.

1. Introduction

Forest fires are one of the main causes of deforestation worldwide, threatening biodiversity. After fire in tropical montane forests, deforested areas are often colonized by the fern *Pteridium* spp. (hereafter bracken) (Hartig & Beck, 2003). Bracken dominates the vegetation for long periods and impairs forest regeneration and seedling establishment (Hartig & Beck, 2003) (Hartig & Beck, 2003). Some studies suggest that bracken can delay natural regeneration due to its dense frond canopy, leaf litter accumulation, and allelopathic effects (De Jesus Jatoba et al., 2016; Le Duc et al., 2007; Marrs et al., 2000). Previous studies in the tropics suggest that forest regeneration in bracken-dominated areas is mainly hindered by seed limitation (Gallegos et al., 2016, 2024; Mayta et al., 2024). Accordingly, low species richness and density of forest species in the seed rain (Mayta et al., 2024; Saavedra et al., 2015), soil seed bank (Lippok et al., 2013), and seedling community was found in bracken-dominated areas (Gallegos et al., 2016; López et al., 2024; Ssali et al., 2017, 2018). So far, little is known about the contribution of the soil seed bank (SSB) to the regeneration of tropical montane forests in areas dominated by bracken (Lippok et al., 2013; Ssali et al., 2018; Xavier et al., 2016).

Since bracken is considered a difficult plant to control (Marrs et al., 1998, 2000), classic management strategies such as cutting off fronds and removing leaf-litter have been used to foster the emergence of some other species (Lowday & Marrs, 1992; Marrs et al., 1998). In this way, fast-growing seedlings were transplanted and successfully grew after the frequent pruning of bracken fronds (Douterlungne et al., 2010). Similar strategies were applied in the Atlantic montane forest, where bracken biomass was reduced after intensive mechanical removal of it's fronds but with limited forest recovery in terms of SSB and natural recruitment (Xavier et al., 2023). Other studies in tropical montane forest found higher seedling recruitment and survival rates of late-successional species in the presence of bracken fronds and litter than after their removal (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2018). In contrast, some pioneer species grew better in completely open areas in Africa (Ssali et al., 2018), while early-successional tree species were favored in bracken-dominated areas in South America (Gallegos et al., 2016; López et al., 2024). Although the effects of bracken management on seedling establishment have been previously studied (Gallegos et al., 2016; López et al., 2024), little is known about the effects of these management strategies on the SSB. In bracken-dominated ecosystems, the fronds form a canopy and provide shade, thereby reducing temperature, and the leaf litter improves soil moisture retention (Gallegos et al., 2015; López et al., 2024). The conditions provided by bracken are favorable for the emergence and germination of late-successional seedlings (Gallegos et al., 2015; Ssali et al., 2018), while pioneer species require higher light conditions to germinate and thrive in open areas (Holl et al., 2000; Williams-Linera et al., 1998). In contrast to the seeds of pioneer and herbaceous species in temperate regions, which often build up SSB (Dalling & Brown, 2009), many recalcitrant seeds of tropical humid forests are not stored in the SSB, because many of them do not experience desiccation at the parent plant, and eaither germinate or perish immediately after dispersal (Bazzaz & Pickett, 1980; Holl et al., 2000; Khurana & Singh, 2001; Ley-López et al., 2023; Moles et al., 2000).

Due to the often-proved dispersal-limitation in the regeneration of tropical montane forests, it would be important to know how the SSB patterns of abundance, richness and diversity are altered by bracken management strategies. The aims of this study are: (a) To evaluate the effect of habitat type on the abundance, richness and diversity of the SSB (b) To compare the species richness, diversity and abundance of the SSB under different bracken management strategies and (c) to compare the abundance, richness and diversity in the SSB between life-forms (tree and non-tree), and dispersal syndromes (zoochorous and anemochorous species).

Because bracken fronds reduce temperature, leaf litter maintains soil moisture (Gallegos et al., 2015; López et al., 2024), and dry conditions increase seed mortality in the soil (Ooi, 2012), we expect to find lower seed abundance, richness and diversity in the absence of fronds and leaf litter. We also expect that in treatments without bracken intervention, and into the forest interior, SSB will increase in abundance, richness and diversity (Lippok et al., 2013). Since seedling recruitment of trees, especially of mid- and late-successional species, increases in the presence of bracken due to the improvement in microclimatic conditions (López et al., 2024), we expect a higher abundance, richness and diversity of trees in the SSB of treatments where fronds and litter are present. Because animal-dispersed species are dispersal limited in bracken-dominated areas (Mayta et al., 2024) and are generally less tolerant of solar radiation (Ley-López et al., 2023), it is likely that the abundance, richness and diversity of zoochorous species will decrease in the frond and litter removal treatments.

2. Methods

2.1 Study area

The study was conducted in the vicinity of Chulumani and Irupana villages, Sud Yungas province, La Paz, Bolivia (16°24’S, 67°31’W). The study area is located in the eastern slope of the Andes, in the tropical montane humid forest, between 1,800 and 2,350 m of elevation. The landscape corresponds to mature forest fragments only in the top of the mountains surrounded by fire-degraded areas in different successional stages and coca leaf crops (*Erythoxylum coca*) for traditional use (Beck et al., 2024; Gallegos et al., 2016; Lippok et al., 2013). Deforested areas are often dominated by bracken (*Pteridium esculentum* subsp. *arachnoideum*) and shrubs, or grasses in more degraded environments (Beck et al., 2024; Gallegos et al., 2016)). Our study area includes the Apa-Apa Mountain which is a floristic hotspot with high conservation value (Beck et al., 2024)**.**

2.2 Sampling design

At eight study sites, separated by at least 1 km between each other, one plot of 50 x 50 m was installed in areas dominated by bracken. These areas were burned for the last time between five and 15 years before our experiment. Each plot was installed at 100 m from the forest edge. Each plot was divided in four subplots, each comprising one of the following management strategies to control bracken: (a) with fronds and with litter (i.e. intact bracken, F+L+); (b) with fronds and without litter (i.e. litter removed manually, F+L-); (c) without fronds and with litter (i.e., fronds were cut with machete every three months for two years, F-L+); (d) without fronds and without litter (F-L-); and (e) forest interior, as a control. The plots were installed in 2019 to analyze the effects of bracken fronds and leaf litter on the species diversity and composition of seeds and seedlings after passive and active restoration. Further details about the study design can be found at López et al. (2024).

2.3 Soil sampling and seed germination monitoring

Between September and October 2021, soil samples were collected at the eight study sites. In each treatment, five soil samples of 15 x 15 cm and 5 cm depth were randomly collected (Dalling et al.,1997). These samples were then mixed to sow three sub-samples per treatment per site in a tree-nursery at the Santiago de Chirca Biological Station (16°23’50.35” S, 67°34’53.47” W, 2,080 m asl). The soil subsamples were arranged in 40 x 30 x 12 cm plastic trays, evenly spread to a depth of 6 cm, and arranged randomly under a 70% shade-net; each tray received periodic watering. Additionally, we randomly set five trays of autoclaved soil of the same dimensions, as a control to record the emergence of seedlings that directly reached the tree-nursery.

The SSB was evaluated using the seedling emergence method (Brown, 1992; Gomes et al., 2019; Price et al., 2010), every 20 days throughout eight months. The seedlings were counted by morphospecies and then all samples were collected and dried for their identification at the Herbario Nacional de Bolivia (LPB).

2.5 Data analysis

We analyzed the entire data set as a whole, to explore general trends, and subsequently divided it into categories, classifying seedlings based on their life form (trees and non-trees) and dispersal syndrome (anemochorous and zoochorous), and analyzed each dataset independently. Seedlings were classified according to previous studies in the area (Gallegos et al., 2016; López et al., 2024) and expert knowledge. Herbs and shrubs were included in the non-trees category. Since the sampling unit was the subplot, we pooled the seedlings originating from each subplot for the analyses. In separate models, we included SSB seedling abundance, species richness and diversity as response variables, and habitat type (forest and the F+L+ treatment, as the bracken area without intervention) as the fixed independent variable. For abundance and species richness, we performed generalized linear mixed-effects models (GLMM) and generalized linear models (GLM), with a Poisson distribution and a log-link function, and a negative-binomial distribution in cases of overdispersion. For species diversity, we used the Inverse Simpson Index with linear mixed models (LMM) and linear models (LM). All models included site as a random effect, except those that had singularity, from which the random effect was removed (Barr et al., 2013).

Then, we analyzed the influence of bracken fronds and litter on the abundance, species richness and diversity of the SSB, in separate models, following the same structure than for habitat type, but including fronds (presence and absence) and litter (presence and absence) as the fixed effects. All these analyses were performed with the package lme4 (Bates et al., 2015). To select the most important variable on the influence of the bracken fronds and litter removal, we performed a model selection, where we selected the model with the lowest AICc (Akaike Information Criterion corrected for small samples) as the best model using the function dredge from package MuMIn (Barton, 2023). Finally, we calculated *P* values from log-likelihood ratio tests (LRT), comparing each model with a null model, using the package MuMIn, and we calculated the marginal R-squared for each model. All analyzes were carried out in R (R Core Team, version 4.3.1, 2023).

3. Results

3.1 Soil seed bank characteristics

We recorded a total of 3,177 seedlings (2,549 in bracken-dominated areas and 628 in forest soil samples) from 31 families and 134 species (Table S3). We identified 68% of all seedlings at the species level, 11% at the genus level, 18% at the family level, and 3% were not identified. The most abundant families were Asteraceae (with 737 seedlings: 672 in bracken-dominated areas and 65 in the forest), Poaceae (577 seedlings: 472 in bracken-dominated areas and 105 in the forest) and Melastomataceae (487 seedlings: 39 bracken-dominated areas and 96 in the forest).

We found more herbs in the total SSB, in bracken-dominated areas and in the forest, than other life forms. The number of trees was lower compared to shrubs and herbs in the total SSB and in bracken-dominated areas; however, it was higher than the number of shrubs in the forest (Table S1). There were more seedlings of anemochorous species than zoochorous species in the total SSB, bracken-dominated areas and in the forest (Table S1).

3.2 Soil seed bank differences between habitats

Soil seed bank abundance, richness and diversity of all emerged seedlings did not differ between habitat types (total abundance: $\chi^2_{3\text{-}4}$= 0.39, R^2= 0.02, LRT: P= 0.52; total richness: $\chi^2_{2\text{-}3}$= 0.637, R^2= 0.02, LRT: P= 0.42; total inverse Simpson index: $\chi^2_{3\text{-}4}$= 0.82, R^2= 0.007, LRT: P= 0.36; Figure 1a-c). The same pattern was observed for trees, anemochorous and zoochorous diversity (trees: $\chi^2_{3\text{-}4}$= 1.73, R^2= 0.02, LRT: P= 0.19; anemochorous: $\chi^2_{2\text{-}3}$= 1.55, R^2= 0.09, LRT: P= 0.21; zoochorous: $\chi^2_{2\text{-}3}$= 3.14, R^2= 0.18, LRT: P= 0.08, Figures 1f and 2c, f).

The abundance of tree and zoochorous species were 7.51 and 2.67 times higher in the forest than in the bracken area without intervention (F+L+), respectively (Figures 1d and 2d). Likewise, species richness of tree and zoochorous species were 1.94 and 1.69 times higher in the forest than in the bracken area, respectively (Figures 1e and 2e). However, the abundance and richness of non-tree and anemochorous species were higher in the bracken area, being 1.45 and 1.54 times higher in abundance and 1.34 and 1.48 times greater in richness, respectively, compared to the forest (Figures 1g, h and 2a, b). Additionally, the diversity of non-tree species in the bracken area was 1.27 times higher than that observed in the forest (Figure 1i).

3.3 Effects of fronds and litter removal on abundance, richness and diversity of the soil seed bank

Bracken fronds and litter removal did not affect total, tree, non-tree and anemochorous species abundance (Figures 1 a, d, g and 2a, Table S2). The abundance of zoochorous species was 2.7 times lower after bracken frond removal than when it was present (Figure 2d, Table S2). Total species richness was 1.4 times lower after removal of bracken fronds and litter compared to the treatment with fronds and litter (Figure 1b, Table S2). Litter removal had a negative impact on tree species richness, reducing it by 2.2 times (Figure 1e, Table S2). Similarly, frond removal negatively affected anemochorous richness,

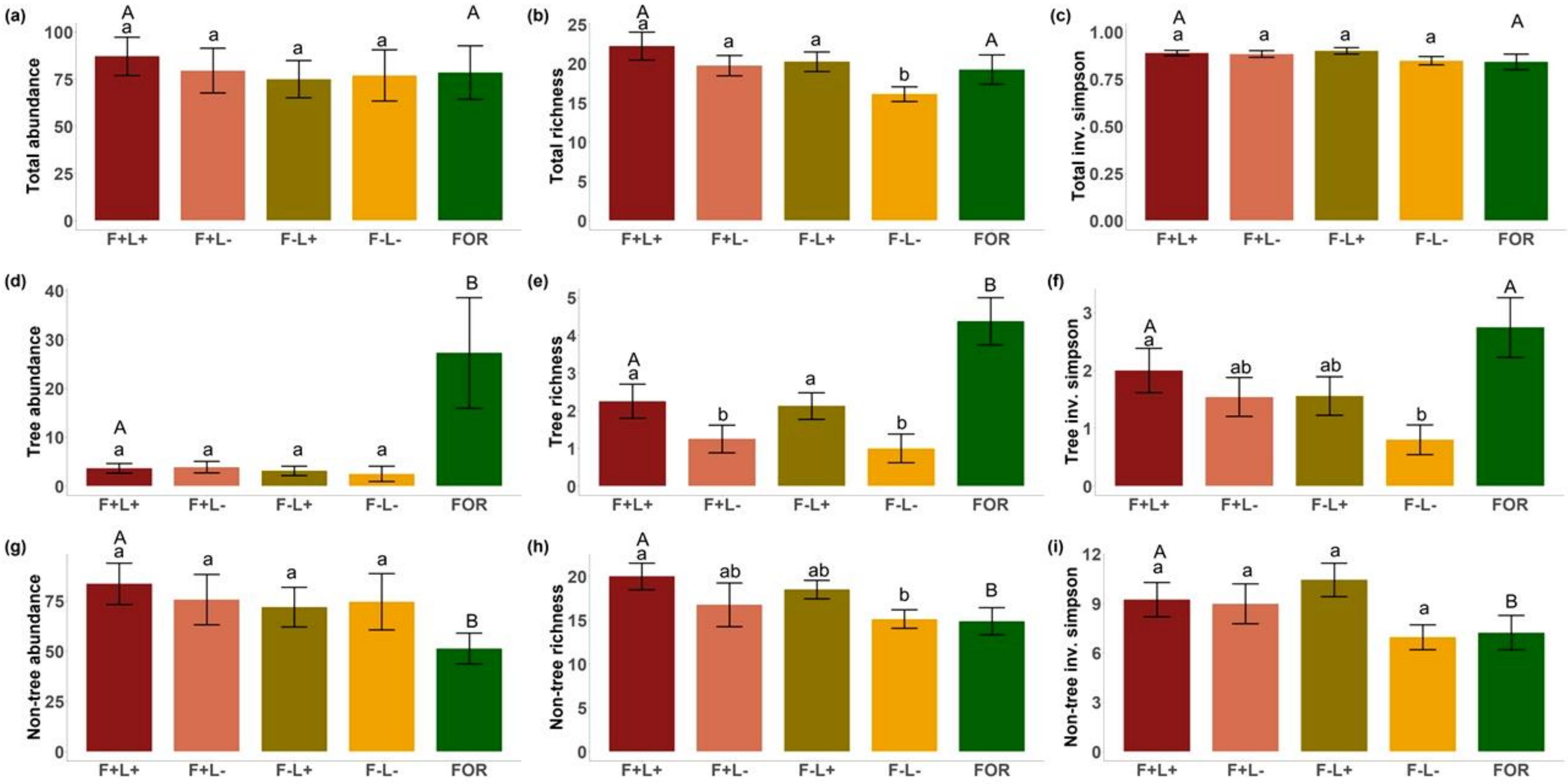

Figure 1. Effects of *Pteridium* fronds (F) and litter (L), presence (+) and removal (-), compared to forest (FOR) on the soil seed bank in terms of abundance (left column), richness (medium column) and inverse Simpson index (i.e. diversity, right column) of (a-c) all species, (d-f) tree species, (g-i) non-trees species. Shown are means ± SE. Different lowercase letters indicate significant differences between the bracken management treatments ($P<0.05$). Different capital letters show significant differences between the forest and the bracken area without intervention ($P<0.05$).

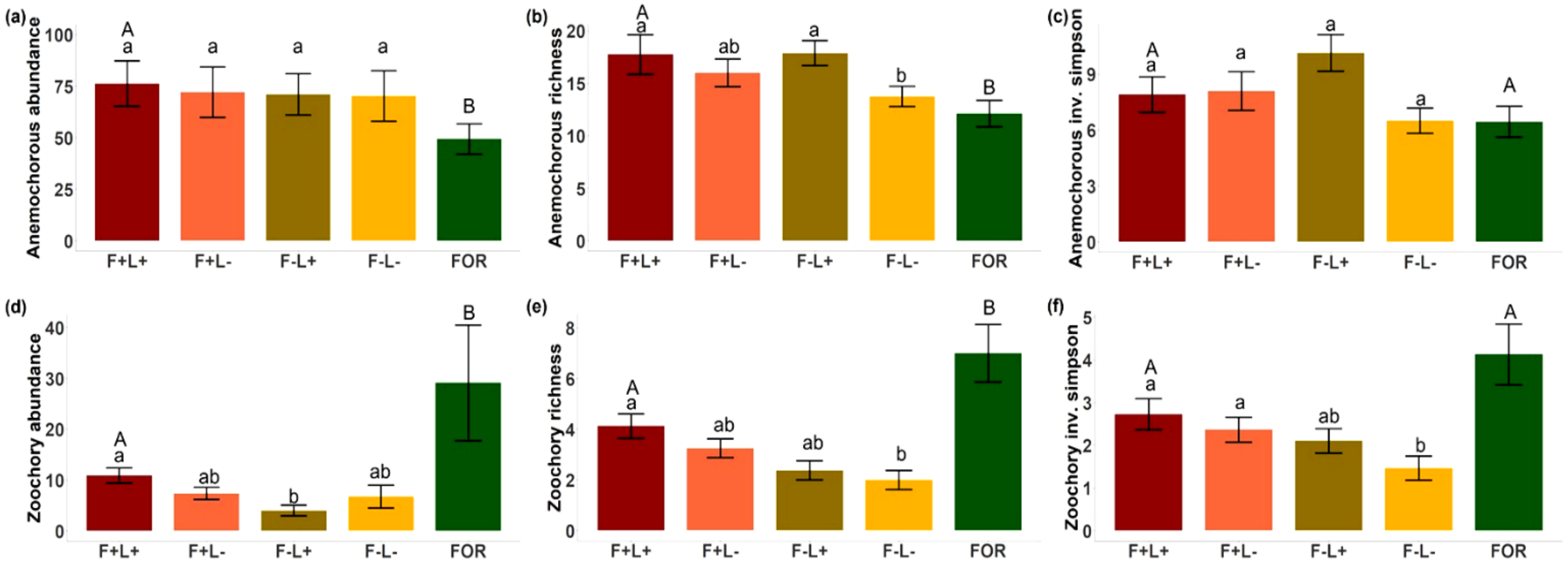

Figure 2 Effects of *Pteridium* fronds (F) and litter (L) presence (+) and removal (-), compared to forest (FOR) on the soil seed bank in terms of abundance (left column), richness (medium column) and inverse Simpson index (i.e. diversity, right column) of (a-c) anemochorous species, (d-f) zoochorous species. Shown are means ± SE. Different lowercase letters indicate significant differences between the bracken management treatments (*P*<0.05). Different capital letters show significant differences between forest and the bracken area without intervention (*P*<0.05).

leading to a 1.29-fold decrease (Figure 2b, Table S2). Frond and litter removal reduced 2.1 times the richness of zoochorous species compared to the treatment with fronds and litter (Figure 2e, Table S2). Non-tree species richness did not change significantly after bracken frond and litter removal (Figure 1h).

Bracken frond and litter removal did not affect anemochorous species diversity (Figure 2c, Table S2). On the other hand, frond removal negatively affected the total and non-tree species diversity, reducing them by 1.58 and 1.51, respectively (Figure 1c, i, Table S2). Likewise, the diversity of tree and zoochorous species significantly decreased with bracken frond and litter removal compared to the treatment with fronds and with litter (Figures 1f and 2f, Table S2).

4. Discussion

We assessed the effects of different bracken management strategies on the soil seed bank. We found that the total abundance, richness and diversity were similar between bracken-dominated and forest habitats. However, the abundance and richness of tree and zoochorous species were higher in the forest. Frond and litter removal did not affect the total, tree and non-tree abundance, but their removal decreased species richness and diversity of tree and zoochorous species. Thus, bracken fronds and litter can help create a suitable microclimate that promotes seed viability of these species. In contrast to some previous suggestions, bracken does not have a negative effect on the soil seed bank, and its presence promotes the storage of all species, particularly of tree and zoochorous species.

4.1 Effects of habitat type on the soil seed bank

The similar abundance, richness and diversity of the total SSB between the bracken area without intervention and the forest were also found in previous studies in a Brazilian savannah and in an African low montane forest (Ssali et al., 2018; Xavier et al., 2016). However, our results contrast with Lippok et al. (2013), who found low seed density in the SSB in bracken-dominated areas in our study area. The similar abundance in both habitats could be related to a high proportion of small seeds, especially of anemochorous species, which have higher mobility in deforested areas. A high abundance of small-seeded species in the SSB is common in secondary tropical forests (Dalling et al., 1998) and in deforested areas, where it is mainly comprised by herbs, grasses and other pioneer species (Lippok et al., 2013; Savadogo et al., 2017).

Similar to previous studies (Gallegos et al., 2016; López et al., 2024) the abundance, richness and diversity of non-tree species was higher in the SSB of the bracken area without intervention than in forest. In contrast, tree and zoochorous abundance and richness were significantly higher in forest than in the bracken area without intervention. These results could be associated with the reduction in the abundance and richness of tropical tree species in the SSB after burning (Shi et al., 2022). Because most species in the tropical forests are dispersed by animals (Howe & Smallwood, 1982) and most animal species avoid deforested areas due to a lack of vegetation heterogeneity, food sources, perches and shelter (Holl, 1999; Holl et al., 2000; Wijdeven & Kuzee, 2000; Wunderle, 1997), this pattern could be explained by a drastic reduction of the seed rain with increasing distance from the forest edge, which occurs in bracken-dominated (Mayta et al., 2024; Saavedra et al., 2015; Ssali et al., 2018) and other deforested areas (Wijdeven & Kuzee, 2000). This pattern could also be associated with changes in the species composition of seed-dispersing birds and bats between the two habitats, which would reduce the likelihood of seeds from the forest entering bracken-dominated areas (Gallegos et al., 2024).

4.2 Effects of bracken fronds and litter removal

We found that the total abundance of SSB did not change after bracken frond and litter removal. A similar pattern was observed for tree, abundance, along with the abundance and richness of non-trees species, as well as the abundance and diversity of anemochorous. Similarly, studies in the Brazilian Atlantic Forest and in Cerrado found no differences in SSB abundance between bracken-dominated and not dominated areas (Rodriguez Da Silva & Da Silva Matos, 2006; Xavier et al., 2016, 2023). However, other studies in Great Britain found a lower abundance of viable seeds under bracken litter (Pakeman & Hay, 1996).

Although other studies found that bracken litter layer acts as a mechanical barrier that impedes seed entrance to the soil (Ghorbani et al., 2006), we found that the abundance, richness and diversity of zoochorous species and the richness and diversity of tree species in the SSB were favored by frond and litter presence. This may be due to the microclimate conditions created by bracken to maintain some seeds viable, especially by reducing soil temperature (López et al., 2024). The presence of bracken fronds and litter could favor seed viability in the SSB because soil temperatures can increase by up to 5°C after litter and frond removal (López et al., 2024). Interestingly, the same study found that soil temperatures were similar inside the forest and the treatment with fronds and litter. The high temperatures that result from the removal of bracken fronds and litter could be the main cause of seed desiccation, increasing seed mortality s. Elevated temperatures are also associated with a reduction of seed viability of some dormant species (Ooi, 2012; Ooi et al., 2009).

The lowest richness and diversity of tree and zoochorous species was found in the treatment without fronds and without litter (F-L-), and the highest in the treatment with fronds and litter (F+L+). This pattern may suggest that bracken creates a microhabitat that allows seeds to survive. Similar patterns were found when analyzing seedling recruitment in previous studies at our site (Gallegos et al., 2015; López et al., 2024), suggesting that these species benefit from bracken conditions, at least in the early stages of plant development.

The SSB abundance of tree and non-tree species did not change with the removal of fronds and litter. This pattern may be associated with the high density of anemochorous species that are present in the bracken-dominated areas and include both tree and non-tree species. Anemochorous species are more tolerant of desiccation than most zoochorous species and are more frequently stored in the SSB (Ley-López et al., 2023). On the other hand, the diversity of non-tree species decreased in the absence of litter. This could be related to the presence of zoochorous large-seeded species of shrubs that may benefit from the temperature and humidity (Gallegos et al., 2015; López et al., 2024) provided by bracken fronds and litter (Gallegos et al., 2016). In the studies of Lopez et al. (2024), a similar pattern was observed for seedling recruitment, with early- and late-successional species taking advantage of the environmental conditions provided by bracken fronds and litter.

Although different management strategies, such as frond pruning and litter removal, are frequently used to control bracken, we found that these techniques do not favor the abundance, richness and diversity of tree and zoochorous species in the SSB. Furthermore, the higher abundance and richness of these groups in the presence of bracken compared to bracken and litter removal are in line with the natural establishment of seedlings in these areas. Our results reflect the low seed rain of these groups associated with dispersal limitation in bracken-dominated areas.

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Chapter IV. Facilitative and competitive effects of bracken fronds and litter on tree seedling recruitment

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Abstract

Tropical montane forests are diverse ecosystems increasingly threatened by land-use change and frequent uncontrolled fires caused by humans. After these fires, affected areas are often dominated by ferns of the genus *Pteridium* (bracken), delaying the rate of forest regeneration. This study examined the facilitative and competitive roles of bracken fronds and litter on seedling establishment, recruitment success, and growth after 36 months, and the extent to which these effects depend on seed size in early plant development processes. At eight sites, we conducted seed addition and seedling-transplant experiments in plots established in bracken-dominated areas, using the following treatments: (a) fronds and litter intact (F+L+); (b) fronds intact and litter removed (F+L-); (c) fronds removed and litter intact (F-L+); and (d) fronds and litter removed (F-L-). A total of 46,640 seeds from 24 tree species were sown and 1,070 nursery-raised seedlings transplanted. In treatments with fronds and litter, seedling establishment and recruitment success increased with seed size. In contrast, in the treatment without fronds and litter all the species had low performance. Fronds proved to be highly beneficial for all seed sizes and for all early development processes. Litter, on the other hand, had negative effects on small-seeded species during establishment, but had neutral to positive effects on the recruitment and growth all species. The disadvantage of small seeds under bracken litter may be related to the high light requirements of seedlings, as litter accumulation reduces light transmission. Species with large seeds and shade tolerance benefit from bracken frond cover, suggesting that restoration strategies in bracken-dominated areas should prioritize these species. Moreover, planting seeds or seedlings shortly after fire, in the presence of bracken fronds and before litter accumulation would be most beneficial for tree species. Additionally, seed dispersers play a crucial role in transporting large seeds into bracken-dominated areas, emphasizing the need for an integrated approach that considers biotic and abiotic factors for effective forest recovery.

Keywords: *Pteridium*, restoration strategies, seed addition, tree early development, tropical montane forest

1 Introduction

Tropical forests harbor about 50% of the world's species (Dirzo and Raven, 2003; Pillay et al., 2022). However, their high diversity is threatened by land-use change, which leads to increased deforestation (Achard et al., 2002; Phillips et al., 2017). Agricultural expansion through slash-and-burn techniques often results in uncontrolled fires and extensive fire-deforested areas (Gardner et al., 2009). After fire, some affected regions are dominated by ferns of the genus *Pteridium* (hereafter referred to as bracken) (Marrs et al., 2000). Historically, fire has been a component of the disturbance dynamics in tropical montane forests (Crausbay et al., 2014). However, the frequency and intensity of fires have increased due to human activity and climate change, leading to environments with fire-dependent vegetation (Asbjornsen and Wickel, 2009). In these environments, superdominant species may become established, with particular concern for bracken, which can sustain continuous fire and hinder forest regeneration (Stewart et al., 2008). Bracken is one of most widespread fern genera in the world, present in temperate an tropical regions (Tryon, 1941; Marrs et al., 2000). However, its occurrence and dominance in tropical montane humid forests are mainly associated with disturbances such as abandoned cultivation, and fires which promote its proliferation (Levy-Tacher et al., 2015; Ssali et al., 2017). In tropical bracken-dominated areas, forest regeneration is slow (Hartig & Beck, 2003; Palomeque et al., 2017), and is often disrupted (Christmann et al., 2023), making ecosystem recovery considerably more difficult. However, the role of bracken in forest succession is unclear, particularly whether it favors or competes with other species during the forest regeneration process.

In plant communities, positive (i.e facilitation) and negative (i.e competition) interactions occur simultaneously (Callaway, 1997; Holmgren et al., 1997). Facilitation occurs when the presence of one plant (the nurse) enhances the fitness of another plant (the beneficiary) by improving microclimatic conditions (Holmgren et al., 1997; Callaway, 2002). In contrast, competition occurs when neighboring plants share the same resources, such as light, soil nutrients, water, or space, often resulting in one plant limiting the growth and survival of the other (Grime, 1977). The balance between facilitation and competition can shift depending on the environmental severity and stress tolerance of the species (Bertness & Callaway, 1994; Wang et al., 2014). During the seedling stage, plant mortality is significantly influenced by biotic and abiotic stress (Alvarez-Clare and Kitajima, 2009). Non-living elements, like rocks or litter can create microsites that modify environmental conditions, sometimes facilitating seedling development or, in other cases, inhibiting it, and as a result influencing competitive dynamics (Loydi et al., 2015; Loayza et al., 2017;

Sangsupan et al., 2018). The interaction between the nurse and the beneficiary species can shift between facilitation and competition through early ontogeny (Paterno et al., 2016). Some plants may initially improve seedling establishment (i.e., cotyledon or leaf emergence) (Paterno et al., 2016), and recruitment success (i.e., alive seedlings at the last evaluation) (Barczyk et al., 2024) of certain species but later may compete for resources such as light and soil nutrients (Calcagno-Pissarelli et al., 2023). This dual role highlights the importance of studying the specific effects of bracken fronds and litter to determine whether they act as facilitators or competitors during early recruitment processes.

Bracken can hinder the establishment of other plant species due to shading by its large fronds (Hartig & Beck, 2003; Silva Matos & Belinato, 2010), and also because it produces allelopathic compounds (De Jesus Jatoba et al., 2016). In addition, the deep litter layer of decomposing fronds acts as a barrier and can prevent seeds from reaching the soil, hindering the establishment of seedlings (De Silva and Matos, 2006; Xavier et al., 2016; Carvalho et al., 2022). These patterns suggest that bracken has competitive characteristics that decrease species richness of trees and shrubs as bracken coverage increases (Carvalho et al., 2022; Paz et al., 2022). Although, in tropical regions bracken-dominated areas often show a low diversity and abundance of tree species (Günter et al., 2007; López et al., 2024), it has been found that bracken can improve microclimatic conditions, in comparison to open areas, by reducing photosynthetically active radiation and soil temperature, which particularly benefits shade-tolerant, often non-pioneer and large-seeded species, thereby facilitating their recruitment (Gallegos et al., 2016; Ssali et al., 2019; López et al., 2024). A better understanding of the interactions between bracken and other plant species will help us to identify factors influencing the regeneration of these heavily deforested areas, and to develop effective strategies for promoting forest regeneration.

Functional traits such as seed size play a crucial role in plant regeneration and demography (Violle et al., 2007; Poorter et al., 2008). In particular, larger seeds are frequently associated with higher recruitment success, lower mortality and slower growth (Leishman and Westoby, 1994; Moles and Westoby, 2004; Poorter et al., 2008). Seedlings from large seeds tend to have a better performance under different establishment hazards, such as deep shade, competition, defoliation, drought, nutrient shortage, herbivory, and burial under litter or soil (Moles and Westoby, 2004). These traits make them particularly advantageous in environments with high competition or challenging abiotic conditions. Conversely, seedlings from small-seeded species tend to grow faster and are often favored in open environments such as forest gaps, where rapid growth is advantageous (Grubb et al., 2013). Seed size is also closely linked to dispersal strategies and their demographic consequences. Large seeds, are often dispersed by animals (e.g., birds or mammals), and may benefit from directed dispersal to favorable microsites, enhancing recruitment success. In contrast, small seeds, commonly dispersed by wind, tend to prioritize dispersal distance over establishment probability (Eriksson and Ehrlén, 1992). Understanding the effect of seed size on seedling performance is particularly relevant in disturbed environments such as bracken-dominated areas, where dense litter layers, intense light competition, and microclimatic conditions strongly influence seedling establishment. However, the role of seed size in shaping regeneration patterns in these ecosystems remains underexplored.

This study aims to evaluate the effect of bracken fronds and litter on the performance of tree species during early recruitment processes. Specifically, we aim to 1) compare the effects of bracken fronds and litter on different early phases of development of tree species, including seedling establishment, recruitment success and growth, according to seed size. We expect that early seedling performance, including establishment, recruitment and growth will have a positive relationship with seed size in the presence of bracken fronds and litter, because large-seeded species are often better adapted to shaded environments (Gallegos et al., 2015; Ssali et al., 2019; López et al., 2024), 2) Assess the intensity and direction of interactions between bracken fronds and litter on seedling establishment, recruitment and growth as a function of seed size. We hypothesize that the shaded environment created by bracken fronds facilitates the establishment, recruitment and growth of species with large and medium-sized seeds due to their greater shade-tolerance and higher reserves, while bracken fronds compete with small-seeded species for light, thereby affecting their development (Milberg et al., 2000; Baraloto et al., 2005). Regarding bracken litter, we expect that the establishment, recruitment and growth of seedlings of medium- and large-seeds will be facilitated due to the higher moisture content in soils with litter (López et al., 2024). However, as small-seeded species often require high light conditions for germination (Milberg et al., 2000; Pearson et al., 2002), the additional shade created by bracken’s litter could impede their establishment and recruitment. Additionally, we expect that litter accumulation creates a physical barrier that smaller seeded species cannot overcome, hindering their growth (Ghorbani et al., 2006; Ssali et al., 2019). 3) Identify potential bracken management strategies to optimize conditions for seedling establishment, recruitment and growth to promote forest succession. To our knowledge, this is the first study that experimentally evaluates the differential effects of fronds and litter on the early stages of tree seedling performance in bracken-dominated areas.

2 Materials and Methods

2.1 Study area

The study was conducted between 2019 and 2023 in the tropical montane humid forests in the Bolivian Andes, in the vicinities of Chulumani and Irupana localities, Sud Yungas, La Paz, Bolivia (16º24’37” S, 67º31’37” W and 16º27’24” S, 67º25’50” W), between 1,850 and 2,450 m asl (Supplementary Figure 1). The mean annual temperature is 20.5°C and the mean annual precipitation is about 1,390 mm (Molina-Carpio et al., 2019). Due to frequent and uncontrolled anthropogenic fires and the expansion of *Erythroxylum coca* plantations, the montane forest have become highly fragmented (Killeen et al., 2005, 2008; Beck et al., 2024).

The only two large remaining patches of continuous primary montane humid forest in the area, located at the top of the mountains, cover approximately 1,200 and 4,000 ha, respectively (Lippok et al., 2014; Beck et al., 2024). These forests are dominated by tree species such as *Alchornea brittonii*, *Beilschmiedia latifolia*, *Couepia* sp. nov., *Coussapoa david-smithii*, *Ficus crassiuscula*, *Hedyosmum cuatrecazanum*, *Ladenbergia oblongifolia*, *Miconia plumifera*, *Pectinopitys harmsiana*, *Piper bolivianum*, *Tetrorchidium andinum*, *Weinmannia rhoifolia* and different tree ferns (Beck et al., 2024). Surrounding these forests are extensive areas dominated by the bracken fern *Pteridium esculentum* (Schwartsburd et al. 2018), wind-dispersed trees such as *Clethra scabra* and *Weinmannia sorbifolia*, shrubs like *Baccharis* spp., and some animal-dispersed tree species like *Myrsine coriacea*, *Piper elongatum* and *Clusia trochiformis*, and shrubs like *Miconia* spp., *Gaultheria* spp. and *Rubus boliviensis* (Lippok et al., 2013; Beck et al., 2024). Bracken covers more than 70% of the vegetation, reaching heights of 150-300 cm (Gallegos et al., 2015; Beck et al., 2024), whit its litter covering approximately 70% of the soil, with a depth between 10-50 cm (Lippok et al., 2013; López et al., 2024).

2.2 Experimental design

We selected eight bracken-dominated areas at 100 m from the forest edge (Figure 1A) that had last burned between five and 15 years prior to the experiment and were each at least 1 km apart. The selected sites had similar vegetation structure and slope aspect. At each site, 50 x 50 m plots were established and divided into four 25 x 25 m subplots using a randomized-block design with the following treatments: 1) fronds and litter intact (F+L+);

2) fronds intact and litter removed (F+L-); 3) fronds removed and litter intact (F-L+); and 4) both fronds and litter removed (F-L-) (Figure 1B). To maintain the treatments, fronds were carefully cut at ground level with a machete every four months, and litter was removed manually.

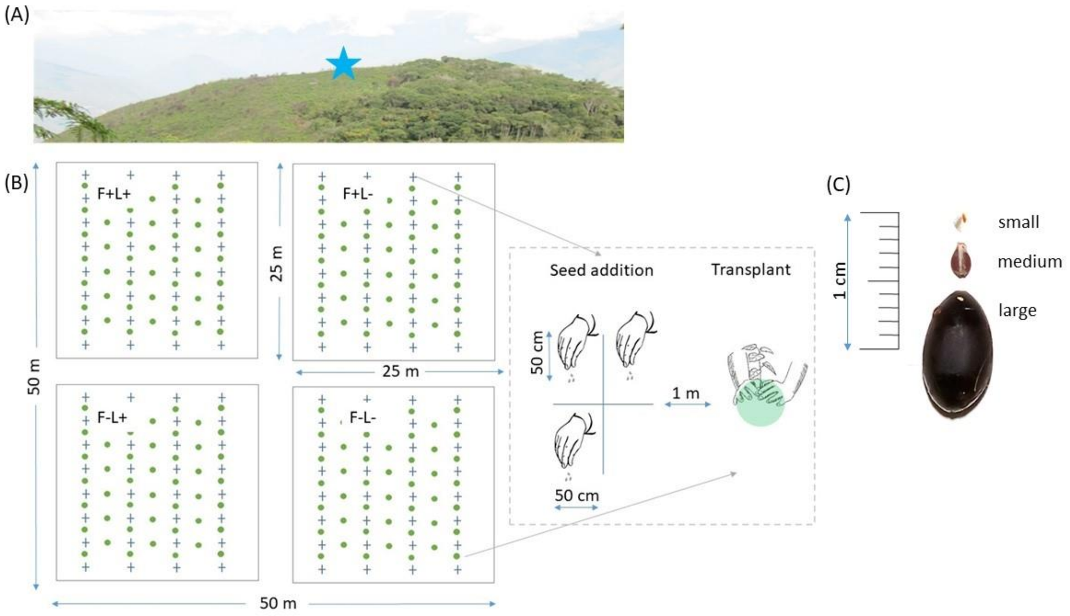

Figure 1. Detailed experimental design for the direct seed addition and transplant experiments with 24 species. (A) Photograph of a bracken-dominated area where the subplots were established, representing different sites (n= 8), (B) Schematic overview of plots and subplots for treatments: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed, and design of seed addition, and transplant experiments: blue crosses represent quadrats where three species were sown, and green circles represent seedlings from the same cohort transplanted one year after being nursery-raised, interspersed with the sown seeds (C) From top to bottom: examples of small-seeded species (<2 mm), medium-seeded species (2-7 mm), and large-seeded species (>7 mm).

The environmental conditions varied across bracken management treatments (López et al., 2024). For instance, soil temperature in treatments without fronds and litter is approximately 8°C higher than in treatments where fronds and litter are present. Similarly, soil moisture is about 15% lower after bracken removal, and photosynthetically active radiation (PAR) at 20 cm above the ground is nearly 80 μmol m^{-2} s^{-1} higher in treatments without fronds compared to those with bracken cover.

2.3 Seed addition and seedling transplant

Based on fruit availability in the study area, 24 common tree species at forest edges and in the forest interior were selected. To enhance response diversity in the experiment, we included species from different families and seed sizes (Palma and Laurance, 2015). (see Supplementary Table 1) for details of species, seed size and number of seeds sown). Seeds were collected from at least ten individuals per species and mixed. All seeds were manually cleaned and counted before sowing. Orthodox seeds were collected once for sowing at all sites, stored in paper bags, and sown within one month. Recalcitrant seeds were collected shortly before sowing at each of the eight sites, and stored in small flasks with damp paper to maintain moisture until sowing within the next two days. In each subplot, seven rows were cautiously delineated to avoid bracken disturbance (Figure 1B). Four rows were designated for the seed addition experiment. In each row, eight 1x1 m2 quadrats were established and further divided into four 50 x 50 cm2 sub-quadrats, leaving the lower right sub-quadrant free to facilitate the evaluation of the other three sub-quadrats. These quadrats were separated by 2 m vertically and 3 m horizontally, with a pathway between rows. Because seed germination and survival are positively related to seed size, and small-seeded species tend to produce more seeds (Westoby et al., 1996; Moles and Westoby, 2004), in each sub-quadrant, a different species was sown at different quantities, depending on their seed size and availability, approximately 50 seeds for small-, 15 for medium- and 3 for large-seeded species (Supplementary Table 1). Seeds were dropped to simulate natural dispersion. A total of 46,640 seeds were sown, of which 32,320 (69.3%) were small seeds, 13,376 (28.7%) were medium-sized seeds, and 944 (2%) were large seeds.

Simultaneously, seeds from the same cohort were sown at the greenhouse from the Santiago de Chirca Biological Station (16º23’50.23” S, 67º34’53.53” W, 2080 m asl), with a 50% shade mesh and regular watering, and grown in separated bags. One year later, nursery-raised seedlings were transplanted to the plots in three rows adjacent to the rows with the seeds added (Figure 1B). Both experiments were implemented in the rainy season (November 2019 - February 2020) to promote germination and survival (Paterno et al., 2016). Due to the high asynchrony of fruit production in the tropics (Usinowicz et al., 2012) and the lower germination and survival rates of some species (Moles and Westoby, 2004), it was not possible to obtain seedlings from all 24 species to transplant. Therefore, only 14 species were used for the transplant experiment (Supplementary Table 1).

For the seed addition experiment, we assessed seedling establishment and recruitment success. Seedling establishment was calculated as the proportion of sown seeds that developed cotyledons or leaves. Recruitment success was calculated as the proportion of the established seedlings that survived to the final assessment (i.e., after 36 months) (Paterno et al., 2016; Barczyk et al., 2024). Measurements were taken at 6, 12, 24 and 36 months, with a focus on the cumulative outcome at 36 months. For transplanted seedlings, the first evaluation of height took place immediately after planting, with subsequent evaluations of seedling growth after 24 and 36 months. Growth was calculated as the difference between the final and initial height of the transplanted seedlings (Paterno et al., 2016).

2.4 Statistical analysis

To assess the changes in early ontogenetic stages of seedlings across the four bracken management treatments according to seed size, we first conducted separate generalized linear mixed-effects models (GLMMs) for each treatment, treating seed size as a continuous variable. Seedling establishment and seedling recruitment were analyzed using a beta-binomial error distribution to account for over-dispersion (Crawley, 2012), while growth was modeled with a Gaussian distribution. Secondly, we classified species by seed-size categories as follows: small-seeded species (n=8, seed size <2 mm), medium-seeded species (n=13, seed size 2-10 mm), and large-seeded species (n=3, seed size >10 mm). We then performed three separate GLMMs using the same response variables, with bracken treatments, seed-size category, and their interaction as fixed effects, and site as a random effect. Additionally, we conducted separate models for each of the 24 species, using only treatment as a fixed effect and site as a random effect.

To assess the intensity and direction of the interaction between bracken fronds and litter, we used the Relative Interaction Intensity Index (RII), which quantifies the relative effect of the species interactions, ranging from -1 (maximum competition) to +1 (maximum facilitation), while values near to 0 indicate neutral interactions (Armas et al., 2004). The RII was calculated based on the performance of the planted seedlings in the different bracken treatments, using the formula:

$$\mathbf{RII} = \frac{\boldsymbol{B_W - B_0}}{\boldsymbol{B_W + B_0}}$$

where BW represents the performance of each ontogenetic stage and seed size category in the presence of bracken fronds, and B0 represent their performance in the absence of bracken fronds. The same formula was used to assess the effect of litter. We pooled the data from treatments with fronds and litter, respectively. The differences in RII indices for seedling establishment, recruiting success and growth for each seed size category and treatment were tested using generalized linear mixed-effect models (GLMM). In all models we included treatment (fronds and litter), seed size category and their interaction as fixed effects, with sites and species as random effects, and a Gaussian error distribution.

All models were fitted using the ‘*glmmTMB*’ package (Brooks et al., 2017), and each model was validated analyzing residuals in ‘*DHARMa*’ package (Hartig, 2022). Post hoc Tukey comparisons among treatments were conducted with the ‘emmeans’ package and all figures were plotted using the ‘*ggplot2*’ package. Marginal R2 values, representing the proportion of variance explained by the fixed factors were calculated using the r.squaredGLMM function of the ‘*MuMIn*’ package (Barton, 2018). The significance of the fixed factors in each model was assessed using the ‘*mixlm*’ package (Liland, 2019). All statistical analyses were carried out using R, version 4.2.1 (R Core Team, 2022).

3 Results

3.1 Addition of seeds and planting of seedlings

Seedling establishment and recruitment success significantly and positive increased with seed size in all treatments except in the treatment without fronds and without litter, were both demographic variables remained low (Supplementary Figure 2A, 2B, Supplementary Table 2). Seedling growth tended to reduce with seed size in all treatments, but the differences were not significant (Supplementary Figure 2A, 2B, Supplementary Table 2).

Seedling establishment was significantly influenced by treatment (X2 = 158.6, p<0.001), seed size category (X2 = 170.9, p<0.001) and their interaction (X2 = 21.4, p<0.01). Establishment was the lowest in the absence of fronds and litter (F-L-, p<0.001), without an effect of seed size. In contrast, the highest seedling establishment was found in the treatment with fronds and litter for large-seeded species (Figure 2A, Table 1). A similar trend was observed in the treatment with fronds and without litter (F+L-) and in the treatment without fronds with litter (F-L+, Figure 2A).

Recruitment success was significantly influenced by treatment (X2 = 228.4, p<0.001), seed size category (X2 = 19.6, p<0.001) and their interaction (X2 = 15.1, p<0.05). Recruitment success in both treatments without fronds (F-L+ and F-L-) was significantly lower (p<0.001) than in treatments with fronds (F+L+ and F+L-) for all seed size categories (Figure 2B, Table 1).

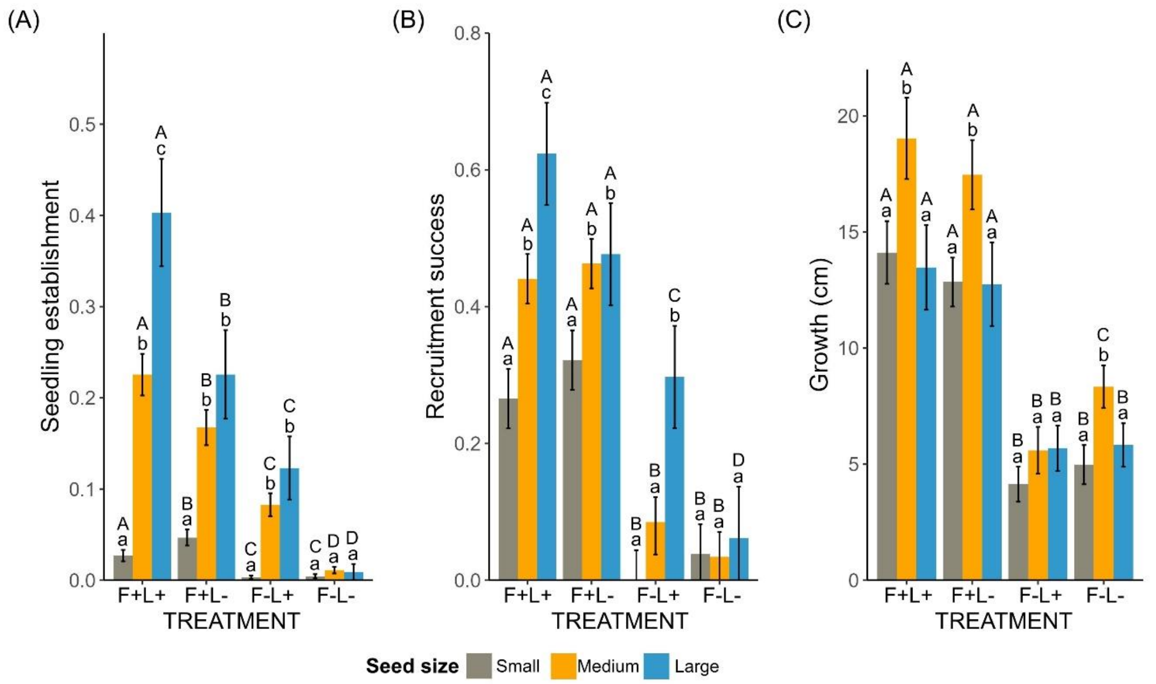

Figure 2. Proportion of (A) Seedling establishment, (B) recruitment success, and (C) growth (after 36 months) according to seed size category in experimental bracken treatments: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots represent predicted values (means ± SE) from the generalized linear mixed-effects models (GLMMs) followed by post-hoc Tukey's multiple comparisons test, P< <0.05. Different capital letters represent significant differences among treatments for each seed size category, while different lowercase letters denote significant differences among seed size categories in each treatment.

From the 1,285 transplanted seedlings, 948 (73.7%) survived the first 36 months. Growth was higher in the treatments with fronds (F+L+ and F+L-) than in the treatments without fronds (F-L+ and F-L-, Figure 2C), and this pattern did not change according to seed size (Figure 2C, Table 1, Supplementary Figure 3). Species specific trends can be visualized in Supplementary Figures and Tables (3-5).

Table 1. Generalized linear mixed effects models (GLMM) for the effect of seed size on a) Seedling establishment, b) Recruitment success and c) Growth, for each treatment analyzed separately. The intercept was set to zero to facilitate comparison. P-values <0.05 are denoted in bold.

	Estimate	Std. Error	Z value	p-value	LRT test p-value	R2 marginal
a) Seedling establishment						
Intercept	3.58	0.23	15.13	**<0.001**	**<0.001**	0.52
F+L-	-0.57	0.27	-2.05	**0.03**		
F-L+	-2.12	0.61	-3.43	**<0.001**		
F-L-	-1.84	0.54	-3.36	**<0.001**		
Medium seeds	2.34	0.24	9.45	**<0.001**		
Large seeds	3.19	0.32	9.77	**<0.001**		
F+L-: Medium seeds	-0.94	0.32	-2.92	**0.003**		
F-L+: Medium seeds	0.95	0.64	1.47	0.14		
F-L-: Medium seeds	-1.41	0.64	-2.19	**0.02**		
F+L-: Large seeds	-1.41	0.45	-3.11	**<0.001**		
F-L+: Large seeds	0.55	0.73	0.75	0.45		
F-L-: Large seeds	-2.47	1.16	-2.11	**0.03**		
b) Recruitment success						
Intercept	0.26	0.04	6.11	**<0.001**	**<0.001**	0.54
F+L-	0.05	0.05	1.03	0.30		
F-L+	-0.26	0.05	-4.83	**<0.001**		
F-L-	-0.22	0.05	-4.15	**<0.001**		
Medium seeds	0.17	0.05	3.24	**0.001**		
Large seeds	0.35	0.08	4.22	**<0.001**		
F+L-: Medium seeds	-0.03	0.07	-0.48	0.62		
F-L+: Medium seeds	-0.09	0.07	-1.27	0.20		
F-L-: Medium seeds	-0.17	0.07	-2.52	**0.01**		
F+L-: Large seeds	-0.20	0.11	-1.82	0.06		
F-L+: Large seeds	-0.06	0.11	-0.55	0.58		
F-L-: Large seeds	-0.33	0.11	-3.00	**0.002**		
c) Growth						
Intercept	2.72	0.20	13.50	**<0.001**	**<0.001**	0.48
F+L-	-0.09	0.06	-1.45	0.14		
F-L+	-1.27	0.25	-4.99	**<0.001**		
F-L-	-1.11	0.24	-4.46	**<0.001**		
Medium seeds	0.31	0.16	1.96	**0.04**		
Large seeds	-0.37	0.19	-1.91	0.055		
F+L-: Medium seeds	0.01	0.07	0.11	0.911		
F-L+: Medium seeds	0.003	0.11	0.02	0.97		
F-L-: Medium seeds	0.21	0.10	2.13	**0.03**		
F+L-: Large seeds	0.03	0.09	0.43	0.66		
F-L+: Large seeds	0.36	0.12	2.92	**0.003**		
F-L-: Large seeds	0.20	0.11	1.70	0.08		

3.2 Intensity and direction of bracken fronds and litter interactions

For all three early recruitment processes and seed-size categories, the relative interaction intensity index (RII) indicated different patterns in both the intensity and direction of interactions. The intensity of facilitative effects was particularly strong for fronds, as the RII values were consistently positive for seedling establishment, recruitment success and growth, for all seed-size categories, indicating beneficial effects (Figure 3, Table 2).

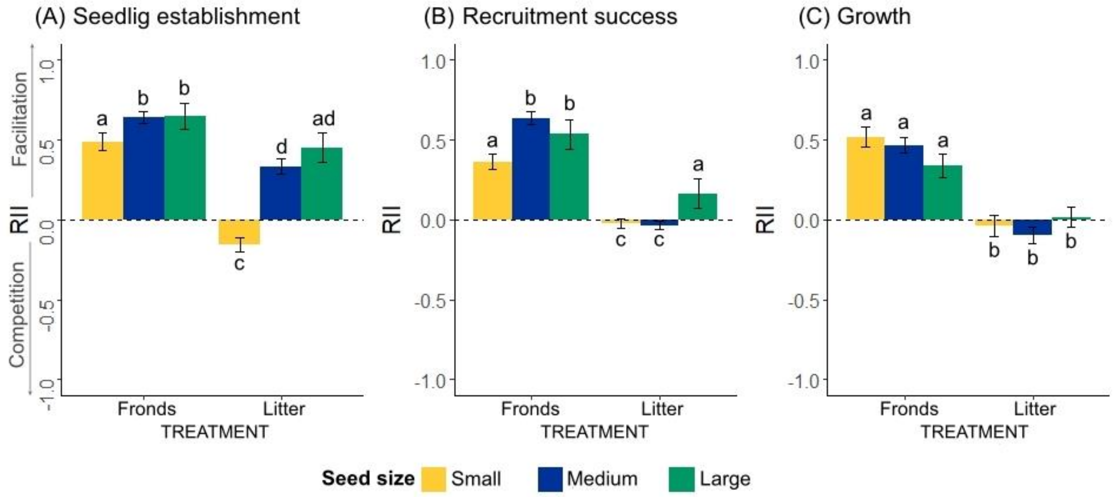

Figure 3. Relative interaction intensity index (RII) between *Pteridium* fronds and litter and (A) seedling establishment, (B) recruitment success, and (C) growth, according to seed size category. The bar plots represent predicted fit values from the generalized linear mixed-effects models (GLMMs) ± SE. Positive values indicate facilitation and negative values indicate competition. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey tests.

On the other hand, the intensity of negative interactions in response to bracken litter was only pronounced for the seedling establishment of small-seeded species, indicating competition, while recruitment and growth showed neutral effects for small-seeded species. In contrast, medium- and large-seeded species showed a strong positive interaction with bracken litter in seedling establishment, indicating facilitative effects. Large-seeded species maintained a positive interaction with litter during recruitment, whereas the interaction was neutral during growth (Figure 3B, C, Table 2).

Table 2. Generalized linear mixed effects models (GLMM) for the Relative intensity index (RII) of a) seedling establishment, b) recruitment success and c) growth. Treatment with fronds and small seeds are in the intercept. P-values <0.05 are denoted in bold.

	Estimate	**Std. Error**	**Z value**	**p-value**	**LRT test p-value**	**R2 marginal**
a) RII Seedling recruitment						
Intercept	0.405	0.053	7.55	**<0.001**	**<0.001**	0.21
Litter	-0.524	0.063	-8.30	**<0.001**		
Medium seeds	0.240	0.060	3.95	**<0.001**		
Large seeds	0.244	0.09	2.49	**0.01**		
Litter: Medium seeds	0.218	0.08	2.53	**0.01**		
Litter: Large seeds	0.32	0.13	2.37	**0.01**		
b) RII Recruitment success						
Intercept	0.318	0.046	6.91	**<0.001**	**<0.001**	0.29
Litter	-0.328	0.051	-6.35	**<0.001**		
Medium seeds	0.326	0.049	6.56	**<0.001**		
Large seeds	0.224	0.079	2.81	**<0.01**		
Litter: Medium seeds	-0.342	0.070	-4.86	**<0.001**		
Litter: Large seeds	-0.043	0.112	-0.38	0.697		
c) RII Growth						
Intercept	0.516	0.070	7.29	**<0.001**	**<0.001**	0.27
Litter	-0.554	0.095	-5.81	**<0.001**		
Medium seeds	-0.049	0.083	-0.59	0.551		
Large seeds	-0.178	0.093	-1.90	0.056		
Litter: Medium seeds	-0.012	0.117	-0.10	0.917		
Litter: Large seeds	0.232	0.132	1.75	0.079		

4 Discussion

We compared the effects of bracken fronds and litter on the performance of tree species at early development phases as a function of seed size. Seed size positively affected seedling establishment and recruitment success, especially in the treatments with fronds and litter. In contrast, most seedlings had low seedling establishment and recruitment success in the treatment without fronds and without litter regardless their seed size. We found a positive effect of bracken fronds in seedling establishment, recruitment success and growth for all seed size categories. In contrast, litter negatively affected the seedling establishment of small-seeded species but had a neutral effect on their recruitment success and growth. These findings suggest that medium- and large-seeded species benefit from the microclimatic conditions created by bracken, specifically from the fronds. We found no significant differences in growth between small- and large-seeded species.

Our results highlight the dynamics between facilitation and competition in bracken-dominated areas, with seed size being a crucial factor for seedling success during establishment, recruitment and growth. Small-seeded species faced a competitive disadvantage to bracken through litter, hindering their establishment, by limiting light and creating a physical barrier. Our results suggest that bracken facilitates most species during their initial stages, but mainly to medium to large-seeded species. These results highlight the importance of understanding the interactions among different plant life stages when evaluating forest regeneration. Our approach emphasizes the need to prioritize medium- and large-seeded species in restoration strategies to promote forest succession in bracken-dominated areas.

4.1 The effect of bracken fronds and litter on early phases of tree development

As expected, bracken fronds and litter influenced the early development of tree species based on seed size. Seed size was positively related to seedling establishment in all treatments except without fronds and without litter. This pattern is consistent with findings where plants with small seeds have lower probabilities of seedling establishment compared to those with large seeds (Leishman et al., 2000; Wang et al., 2022) in shaded conditions, typical of bracken-dominated areas. This occurs because light requirements for germination and establishment decrease as seed size increases (Milberg et al., 2000). Furthermore, large seeds can produce robust seedlings with thicker stems and larger cotyledons, which not only provide nutrients until the first true leaves develop but also, in some species, contribute to photosynthesis, providing an additional energy source that is advantageous in shaded environments (Kitajima, 2003).

In our seed addition experiment we observed significantly higher recruitment of small-seeded species in treatments with fronds and litter compared to those where fronds and litter had been removed. This pattern might become even more evident with an increase in sample size. For instance, Soliz et al. (in preparation) found similar results using the same species, comparing seedling emergence under natural conditions and in a nursery setting. This result can be explained by the higher temperatures and lower humidity in the absence of fronds and litter (Gallegos et al., 2015; López et al., 2024), conditions that may be too harsh for seedling survival. This is consistent with previous findings showing that fronds ameliorate the harsh conditions of open areas by reducing soil temperature and photosynthetically active radiation, thus improving seedling establishment and recruitment (Gallegos et al., 2015; López et al., 2024).

Bracken-dominated areas are characterized by low species diversity (Günter et al., 2007; Ssali et al., 2017; López et al., 2024). However, in addition to *Pteridium*, there is a dominance of some pioneer and small-seeded shrub species, particularly from the Asteraceae, Ericaceae and Melastomataceae families (Lippok et al., 2013). Our results suggest that this lower diversity could be due to the fact that only a few small-seeded species can thrive in these ecosystems, and those that could succeed do not arrive, mainly due to the lack of seed dispersers (Saavedra et al., 2015). Among the small-seeded species in our study, *Miconia hygrophila* (Melastomataceae) exhibited high seedling establishment and recruitment. These results show the variability within small-seeded species, suggesting that other functional traits such as cotyledon type, bark thickness, leaf area, specific leaf area, and wood density, may also play an important role in determining a species ability to thrive in these challenging environments (Green and Juniper, 2004; Moles and Westoby, 2006; Baraloto and Forget, 2007; Poorter et al., 2008), and should be investigated in future studies.

4.2 Intensity and direction of bracken fronds and litter interactions

Our study showed that all seed-size categories benefited from the presence of bracken fronds in the early stages of tree development. All the species, showed improved seedling development under bracken fronds, which highlights the role of bracken as a facilitative species rather than a competitor for resources. These results align with recent research has found that ferns promote community assembly by increasing soil stability and other soil properties and reducing competitive pressures (Azevedo-Schmidt et al., 2024).

The competitive effects of bracken through litter on small-seeded species are consistent with previous findings suggesting that small-seeded species are particularly sensitive to litter barriers (Moles and Westoby, 2004; Jessen et al., 2023). This sensitivity may be related to their limited reserves, which make it difficult for them to penetrate or tolerate litter layers (Aud & Ferraz, 2012; Wang et al., 2022). During the establishment phase, bracken litter particularly disadvantages small-seeded species, which often grow rapidly and require a lot of light (Pereira De Souza and Válio, 2001). In addition to the shade provided by the bracken fronds, the litter creates an even shadier environment that is difficult for small-seeded species to overcome (Molofsky et al., 1992; Loydi et al., 2012). Moreover, seeds can become trapped in the litter layer, preventing them from coming into contact with the soil and reducing their probabilities of germination (Donath and Eckstein, 2012).

Although litter showed a facilitative effect for medium- and large-seeded species during seedling establishment, these effects tend to became neutral over time. This ontogenetic shift is consistent with previous research showing that the intensity and direction of interactions could change during ontogeny (Paterno et al., 2016). These findings emphasize the need for long-term studies to better understand the dynamics of facilitation and competition in ecological restoration efforts.

5 Conclusions and future directions

Our Our findings showed that the presence of bracken fronds and litter creates a complex environment where facilitation and competition coexist, influencing the regeneration dynamics of tropical forests. These results are consistent with previous research, highlighting that larger seeds are more capable of overcoming the physical barrier and low light conditions imposed by bracken (Gallegos et al., 2015; López et al., 2024; Mayta et al., 2024), as these have greater resources to support seedling growth, thereby enhancing their ability to thrive in these low-light conditions (Moles and Westoby, 2004; Baraloto et al., 2005). Given that many studies on plant interactions are limited to short-term observations (Siles et al., 2008), additional monitoring is needed to determine whether Pteridium facilitates long-term recovery and to understand the effect of bracken in subsequent stages of plant ontogeny. As plants mature, their growth rates and resource demands increase, suggesting that the dynamics between neighbors may shift over time (Gómez-Aparicio, 2009). For instance, we found that although litter had facilitative effects for medium- and large-seeded species during seedling establishment, these effects became neutral to negative along time. Since seedlings typically exhibit low growth rates and resource requirements during early stages, demands that intensify as they develop, these requirements could eventually change the intensity and direction of plant interactions (Berkowitz et al., 1995).

Restoration projects and management strategies in bracken-dominated areas should consider the advantages of fronds' facilitative effects and the negative effects of litter accumulation, especially on establishment of small-seeded species, and probably also for medium-and large-seeded species in the longer term. Identifying tree species with traits that favor their successful establishment, recruitment and growth under bracken is essential to inform restoration strategies to accelerate tropical forest succession. Active restoration practices, such as direct seed addition and seedling transplant, could be implemented in recently burned areas, where bracken fronds enhance microclimatic conditions and the absence of litter help mitigate the initial negative effects of bracken litter accumulation. Transplanting seedlings, which have a survival success exceeding 80%, offers a more reliable approach than seed addition in bracken-dominated areas, especially for small-seeded species. However, to enhance seedling performance of nursery-raised seedlings from small-seeded species, probably seedling transplant should be accompanied by frequent bracken mowing, at least during the first year (Douterlungne et al., 2010), making this option difficult to be set in large areas. Selecting and planting large-seeded shade-tolerant species could be a viable approach to enhance forest recovery in areas dominated by bracken. The incorporation of large-seeded species into active restoration efforts enhanced survival rates and improved long-term recruitment success after land abandonment in areas dominated by grasses (Schubert et al., 2024). Long-term studies conducted on abandoned farmland and cattle-grazed areas, showed that active restoration approaches, such as applied nucleation and plantation, significantly enhance the recruitment of large-seeded late-successional species compared to natural regeneration (Schubert et al., 2024).

Since medium and large-seeded species are particularly favored by bracken, and most of them are mainly dispersed by animals, our results emphasize the importance of attracting seed-dispersing animals, as their activity could be crucial for the transportation of large seeds into bracken-dominated areas (Saavedra et al., 2015). Therefore, incorporating animal attractants such as bird perches or planting animal-dispersed plant species may enhance seed dispersal (Saavedra et al., 2015; López et al., 2024; Mayta et al., 2024). In doing so, including an integrated management approach that considers both biotic and abiotic interactions is crucial for restoration strategies.

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Chapter V. A trait-based approach for restoring tropical forest in fire-deforested bracken-dominated areas

This chapter is under review in *Journal of Applied Ecology* as

Gallegos, S. C., **López, C. L.**, Kazuya, N., Solíz, C. A., Fuentes, A. F., Mayta, C., Cayola, L., Tello, S., & Hensen, I. A trait-based approach for restoring tropical forest in fire-deforested bracken-dominated areas

Abstract

1. Human-induced fires create complex conservation problems in tropical areas. After fire, montane tropical deforested areas are often dominated by the bracken fern (*Pteridium* spp.), which impose strong environmental filters, including abiotic (light, soil and air temperature and humidity) and biotic factors (related to plant-plant interactions) on colonizing tree species. Because few tree species are able to overcome these filters, forest recovery is typically a slow and lengthy process.
2. We explored whether a trait-based approach could be used to guide species selection in active restoration projects in bracken-dominated areas. We first tested whether traits could be used to predict which species can overcome bracken-associated filters. We then tested if abundant tree species in old-growth forests, commonly selected for active restoration programs, have high recruitment probabilities in bracken-dominated areas.
3. To identify the key traits, we conducted a seed addition experiment in bracken-dominated areas, of 5-15 years after fire, with 23 tree species common in the Bolivian montane forests, and monitored seed germination, seedling survival and growth for 36 months. We then related seedling performance to their functional traits.
4. We found that eight functional traits improved tree seedling performance in bracken-dominated areas, and that only a few tree species have the required set of traits. Most of the favored traits correspond to conservative strategies. The species dispersed by birds, especially those with large seeds, were the most likely to overcome the filters created by bracken. Based on the trait-predictions, we found that the species predicted to overcome bracken are not always among the most abundant species in old-growth forests. Therefore, active restoration programs should consider trait-based seed addition experiments to guide species selection with higher seedling performance.
5. Synthesis and applications: Our approach can be used by stakeholders to select the species more suitable to be included in active restoration projects in bracken-dominated areas throughout the tropical region.

Key words: Filters, Fire, Functional traits, *Pteridium*, Seed addition, Seedling demography, Trees, Tropical forest

1. Introduction

Tropical forests harbor the highest biodiversity and endemism in the world (Liang et al., 2022; Myers et al., 2000). However, their extraordinary diversity is increasingly threatened by escalating deforestation rates, with human-induced fires to create land for farming being one of the main drivers (Feron et al., 2024; Hansen et al., 2013). After fire or land-abandonment, the bracken fern *Pteridium* spp. often colonizes and dominates the vegetation for long periods (Amouzgar et al., 2022; Carvalho et al., 2022; Ssali et al., 2017; Suazo-Ortuño et al., 2015). Bracken-dominated areas are globally widespread, representing a problem for forest biodiversity, and animal and human health due to its toxic and carcinogenic properties (Vetter, 2009). Due to increasing fire frequency, along with a hotter and drier climate, bracken cover is expanding at an alarming rate (Schneider & Fernando, 2010; Velazco et al., 2024). Furthermore, since bracken creates a large fuel load that is highly flammable (Vega et al., 2024), fires frequently occur at the same sites, further inhibiting forest recovery (Schwartz et al., 2020) are common, highlighting the need to develop conservation and restoration strategies that quickly foster forest recovery.

Forest succession in bracken-dominated areas is mainly hindered by dispersal limitation, i.e., the failure of seeds to reach a site (Münzbergová & Herben, 2005), shown by the reduced species richness and abundance in the seed rain, seed bank, and seedling recruitment within bracken-dominated areas (Gallegos et al., 2016; Günter et al., 2007; López et al., 2024; Mayta et al., 2024; Saavedra et al., 2015; Ssali et al., 2017). As most tropical forest tree species are dispersed by animals (Acosta-Rojas et al., 2023; Howe & Smallwood, 1982), seed limitation has been attributed to differences in the species composition of frugivorous birds and bats between forest and bracken-dominated areas; the lower abundance of seed-dispersing medium- and large-terrestrial mammals in the bracken-dominated areas (Gallegos et al., 2024); the lack of natural perches for seed-dispersing birds (Mayta et al., 2024; Saavedra et al., 2015), and the lower availability of food resources for animals in disturbed areas (Wunderle, 1997).

Dispersal limitation can be overcome by active forest restoration in which seeds/seedlings are planted within bracken-dominated areas. However, bracken also affects seed germination and seedling survival. Bracken produces large fronds and a deep litter layer that together shade other plants and also produces several secondary metabolites against herbivores and UV radiation that may have allelopathic effects (Alonso-Amelot et al., 2004; Jatoba, 2023; Marrs & Watt, 2006). Consequently, only a few shade-tolerant tree species successfully recruit in bracken-dominated areas (e.g. Carvalho et al., 2022; López et al., 2024; Ssali et al., 2017). Active restoration projects need to have evidence-based strategies to select species that can overcome the conditions created by bracken and have the highest likelihood of establishing to begin forest recovery.

A trait-based approach could facilitate the selection of species in active restoration strategies across the tropical region (Fremout et al., 2022). Functional traits serve as indicators of ecological strategies and can be used to generalize species' responses to different environmental filters (Metz et al., 2023; Rüger et al., 2018). Trait-based approaches have been increasingly used in restoration studies during the last decade (Coutinho et al., 2023; Loureiro et al., 2023). To identify the most relevant traits, it is crucial to analyze the relationship between functional traits and plant fitness in a determined environment. Since bracken-dominated areas impose multiple abiotic filters (related to photosynthetically active radiation, soil and air temperature and humidity), and biotic filters (related to plant-plant interactions such as facilitation/competition, potential allelopathy, etc.), a combination of traits may be needed to predict which traits and species are capable of overcoming the bracken filters.

To understand the predictive ability of traits for active forest restoration, we conducted a seed addition field experiment in post-fire tropical bracken-dominated areas with 23 native forest tree species. We asked the following questions: i) Which functional traits allow species to overcome the filters in bracken-dominated areas?. Since bracken fronds and litter shade other plants, we expected that traits related to shade-tolerance would be important, leading to greater success for shade-tolerant, late-successional species (Gallegos et al., 2015, 2016; López et al., 2024; Ssali et al., 2017). Also, since previous studies related the slow forest succession to seed limitation of animal-dispersed species (Gallegos et al., 2016; Mayta et al., 2024; Saavedra et al., 2015), we also expected that species able to persist under bracken are dispersed by animals. ii) Which species are likely to overcome the filters imposed by bracken? According to the favored functional traits, we expect to score the species from the community and select those with the higher probability of recruitment in bracken-dominated areas. iii) Is the abundance of the species in a reference old-growth forest a good predictor to guide species selection in restoration programs? We examined whether species with the highest probabilities of recruiting within bracken-dominated areas are abundant as adults in old-growth forests. Since different filters for seedling recruitment act between bracken dominated areas and old-growth forests, and there is evidence for seed limitation in bracken-dominated areas, we expected that the species favored by bracken will not be abundant in old-growth forests. Therefore, we expected that the active restoration value of the species will not be directly related to their abundance in old-growth forests.

2. Materials and methods

2.1 Study area

The study was conducted in the vicinity of Chulumani village, Sud Yungas province, La Paz, Bolivia (16°24′ S, 67°31′ W, between 1,850 and 2,300 m a.s.l.), on the eastern slope of the Andes. The vegetation corresponds to a tropical montane humid forest, with a mean temperature around 19.5°C and a mean annual precipitation of 1440 mm (registered at 1700 m), with a peak between December and February (Beck et al., 2024). The landscape consists of two large forest remnants, the Apa-Apa and Cala-Cala Mountains of approximately 4,000 and 1,200 ha, respectively. The forest remnants are surrounded by fire-deforested areas mainly dominated by the bracken fern *Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) J.A.Thomson (Schwartsburd et al., 2018), interspersed with shrubs and grasslands (Beck et al., 2024).

2.2 Experimental design

In November 2019, we conducted a seed addition experiment with 23 tree species. Species were selected because they were common in the forest interior and/or at forests edges within our study area (Beck et al., 2024; Lippok et al., 2014), exhibit a wide range of functional traits, and were fruiting when we established the experiment. To obtain the seeds of these species, we collected fruits from at least ten individuals per species in the two large forest remnants in our study area (Fig. S1). Ripen fleshy fruits were stored in a dark and fresh room for up to five days, while dry fruits and seeds were stored for up to 10 days. For each species, we mixed the fruits from different mother trees, cleaned the fruits manually, counted the seeds, and stored them in small flasks with moist paper (fleshy fruits) or paper bags (dry seeds) until sowing the next day.

For sowing in the field, we established eight 25 x 25 m experimental plots in bracken-dominated areas, at least 1 km apart from each and 100 m from the forest edge (Fig. S1). In each plot, we established 32 1 m^2 squares, 3 m apart, and marked with a colored 1-m PVC tube at the center to facilitate relocation. Each square was divided into four sub-squares, oriented upslope. We sowed one of the 23 forest tree species (Table S1) in each of the three sub-squares (0.5 x 0.5 cm, hereafter depots), leaving the fourth sub-square empty for access.

Species were randomly assigned to each depot, ensuring each species was tested four times per plot. In total, there were 96 depots per plot (32 squares x 3 depots). Because seed germination and seedling recruitment were frequently found to be positively related to seed mass/size, and small-seeded species produce more seeds (Leishman, 2001;

Visser et al., 2016), we sowed each species at different densities according to their seed size (Table S1). The seeds were dropped in their assigned depots to simulate natural seed dispersal and watered with a handheld home gardening sprinkler immediately after planting. We monitored seed germination, seedling survival and growth after 6, 12, 24 and 36 months. We minimized the disturbance to the natural structure of the bracken-dominated area during plot setup and measurements.

2.3 Functional traits

We measured the following nine functional traits in at least five adult individuals of each species: maximum tree height (H_{max}, in m), leaf area (LA, in cm^2), specific leaf area (SLA, in cm^2/g), leaf dry matter content (LDMC, in mg/g), bark thickness (in mm), stem specific density (SSD, in mg/mm^3, corrected for secondary branches multiplying by 1.411, Pérez-Harguindeguy et al. 2013), seed size (i.e., seed length in mm), seed mass (in g) and dispersal vector (birds, bats or wind) (Table S1). We defined the main dispersal vector for each species based on expert knowledge, morphology and literature. Since seed size and seed mass were highly correlated (Pearson's $r = 0.86$, $P < 0.001$), we chose to include seed size in our analyses, as it is easier to measure without sophisticated equipment. We measured the same traits in 23 other species common in the study area to apply our results with a larger dataset (Table S1). All traits were collected and measured following standardized protocols (Pérez-Harguindeguy et al., 2013).

Additionally, to select the species with the higher probabilities of recruitment in the community, we used a database from 10 permanent plots (20 x 20 m), established in secondary forests in our study area approximately 20 and 40 years after the last disturbance. These plots contained 1,789 individuals with DBH ≥ 2.5 cm, from 115 species (Missouri Botanical Garden – Bolivia Program, 2024). This database included six traits (SLA, LA, SSD, maximum height, seed size and dispersal vector) from the 95 most common tree and shrub species.

To assess the potential of abundance as a predictor for seedling performance in deforested areas, we related the active restoration value to the abundance of the species found in old-growth forests from the study area (Lippok et al., 2014)**.**

2.4 Data analysis

Seed germination was calculated as the number of seeds germinating within 36 months in relation to the number of sowed seeds. Seedling survival was calculated as the number of seedlings surviving until the end of the experiment (36 months) relative to the number of germinating seeds. We calculated the relative growth rate (RGR) using the formula:

($\ln(h_{t+1}) - \ln(h_t))/t$, where h is the individual height in cm at time t and $t+1$, and t is the time elapsed in days between measurements. To account for the wide data variability in seed size, maximum height and LA, these traits were log-transformed. All traits were scaled to mean 0 and standard deviation 1 before analysis. For all analysis, we used the mean value of each functional trait at the species level.

To assess which functional traits favored seedling performance in the bracken-dominated areas, we fitted generalized linear mixed models (GLMMs), using the package *glmmTMB* (Brooks et al., 2017). Survival and germination were modelled assuming a binomial and a beta-binomial distribution, respectively, to control for overdispersion, while RGR was modelled assuming a Gaussian distribution. All GLMMs included the functional traits as fixed effects and plot as a random effect to account for the experimental design. Initially, we included all functional traits, but after checking for collinearity (by variance inflation factors, VIF), we retained traits that had a VIF less than 3. We also included second-order polynomials for bark thickness and LDMC in the full model after data exploration indicated a non-linear relationship. We performed model selection using the dredge function from the package *MuMIn* (Barton, 2022), and selected the best single model with the lowest AICc for interpretation. In all cases, we checked the residuals with the package *DHARMa* (Hartig, 2022), and assessed overdispersion using the *check_overdispersion* function from the package *performance* (Lüdecke et al., 2021). To assess whether the models can be applied to species not included in our dataset, we analyzed the out-of-sample predictive power of each model using the leave-one-out cross-validation (LOO-CV) and calculated the root mean squared error (RMSE) with the package *Metrics* (Hamner & Frasco, 2018). To visualize the effects of traits from the best models, we plotted the predicted values using the package *visreg* (Breheny & Burchett, 2017), with prediction lines calculated by setting all other variables to their mean values. We defined the trait values necessary to overcome bracken based on the point where each trait exceeded 25% of seed germination, 50% of seedling survival and 0.4 of RGR (hereafter, thresholds). These threshold values were selected to ensure that at least a quarter of the individuals will germinate and half of them will survive after active restoration.

To identify which species are important candidates for active restoration (Figure S1), we calculated a trait-based prediction of their combined ability to germinate, survive and grow in the bracken environment (hereafter, ‘active restoration value’). First, we calculated the marginal R^2 (R^2m) for each best model with the *r.squaredGLMM* function from the package *MuMIn* and the relative importance of each fixed predictor using the package *glmm.hp* (Lai et al., 2022). For each species, we summed the relative importance values of each predictor, when the associated trait for the species surpassed the threshold trait value identified above, and then multiplied the result by the R^2m of the demographic variable. We then summed the values obtained for each demographic variable to obtain the "active restoration value" for the species (an example can be found in Table S2). For the additional 23 species that were not in our experiment, but for which trait measurements were taken, we used the same models to predict their active restoration value as candidate species for restoration. Since we were interested in exploring which other species within the wider community could be candidates for restoration, we calculated the active restoration values in a larger community database.

Finally, to assess if the abundance of the species in a reference old-growth forest is a good predictor of seedling performance, we performed linear regressions between the active restoration values obtained for each species and the abundance (transformed to log10+1) of the species in old-growth forests from the study area (Lippok et al., 2014). All analysis were performed in R version 4.3.0 (R Core Team, 2023).

3. Results

i) Which functional traits allow species to overcome the filters in bracken-dominated areas?

In total, 1,003 seeds out of 13,952 planted seeds germinated in the bracken-dominated areas. Six functional traits explained differences among species in seed germination in bracken-dominated areas, explaining 65% of the total variation (Fig. 1, Table 1, Table S3, S4). Bird-dispersed seeds exhibited higher germination rates than bat-dispersed seeds, although the former did not significantly differ from wind-dispersed seeds. The 25% threshold for seed germination was exceeded only for species dispersed by birds (Fig. 1a). Seed germination was higher than 25% when seeds were larger than 3 mm, leaf dry matter content (LDMC) was less than 357 mg/g, bark thickness was greater than 3.25 mm, specific leaf area (SLA) was less than 78 mm^2/g and maximum tree height was less than 10.5 m (Fig. 1b-f, Table 1).

From the 1,003 germinated seeds, 552 seedlings survived until the end of the experiment. Three functional traits were related to seedling survival, explaining 50% of the variation (Table 1, Table S3, S4). Seedling survival was highest for wind-dispersed species, but seedling survival rates were above 50% for all dispersal agents (Fig. 1g, Table 1). Seedling survival was higher than 50% for species with seeds larger than 3.6 mm and maximum tree height below 11.3 m (Fig. 1h-i, Table 1).

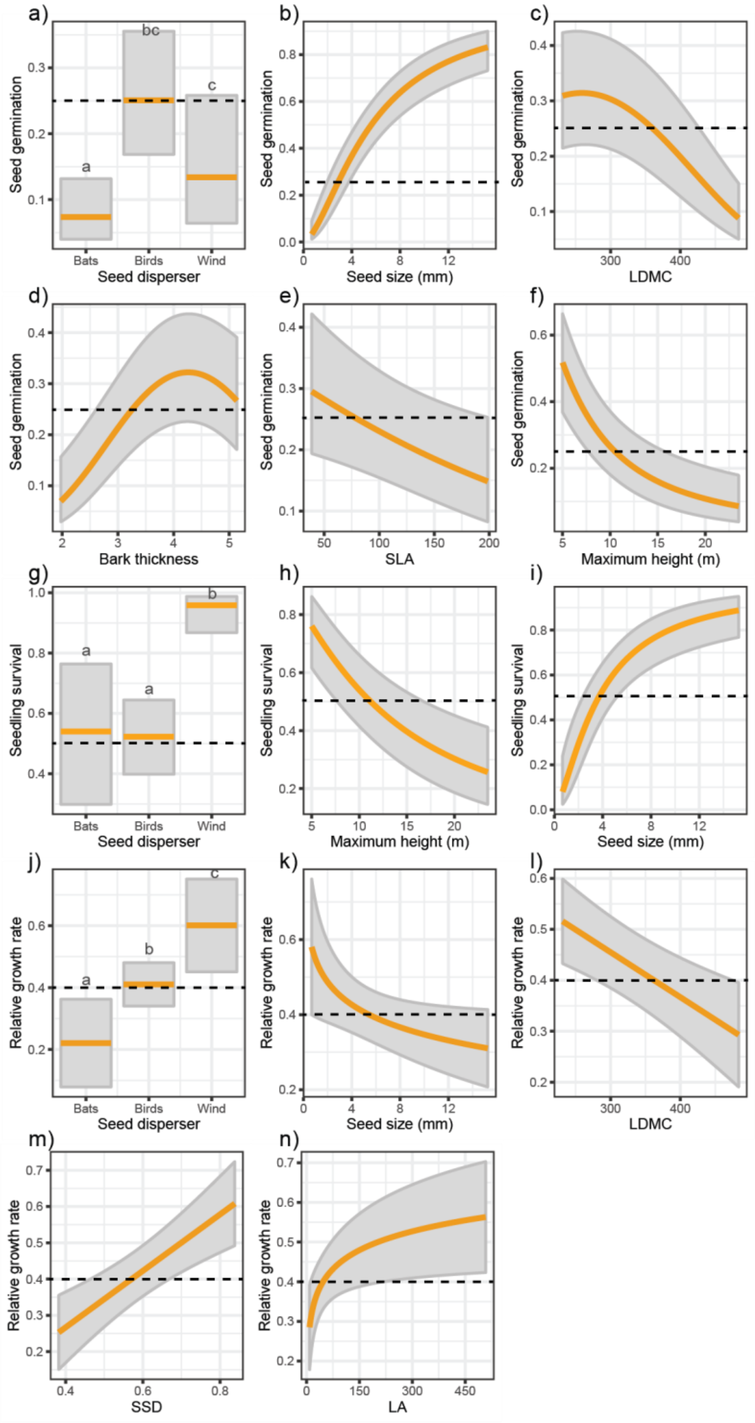

Fig. 1. Relationships between (a-f) seed germination, (g-i) seedling survival, and (j-n) seedling relative growth rate in bracken-dominated areas in relation to functional traits measured on adult plants. Only traits included in the best generalized linear mixed-effects models are shown. The predicted lines (in orange) were determined by setting all other traits to their mean value. The shaded area represents the 95% confidence interval of the prediction. Horizontal dashed lines represent the threshold set for the trait filters (25% of seed germination, 50% of seedling survival and 0.4 of RGR). Full names of the functional traits and units can be found in methods.

Five traits explained 38% of the variation in relative growth rates (RGR) (Table 1, Table S3, S4). The RGR was greater than 0.4 for species with seed size smaller than 5.3 mm, LDMC less than 359 mg/g, stem specific density (SSD) greater than 0.57 g/cm^3, and LA greater than 47 mm^2 (Fig. 1k-n, Table 1). Wind-dispersed species exhibited a higher RGR compared to bird- and bat-dispersed species, with bird-dispersed species showing a higher RGR than bat-dispersed species; both bird- and wind-dispersed seeds had RGR values exceeding 0.4 (Fig. 1j).

Table 1. Variable contributions of all traits included in the best models and the favored trait values for seed germination, seedling survival and growth in bracken-dominated areas. Only the traits present in the best generalized linear mixed-effects models are shown. The trait thresholds to define the favored values were set at 25% of seed germination, 50% of seedling survival and 0.4 of relative growth rate. R^{2}m = marginal R^2, and RMSE = root mean squared error to assess the out-of-sample predictive power for each best model.

Demographic variable	R^{2}m	RMSE	Trait	Variable contribution (%)	Favored trait values	Unit
Germination	0.65	0.13	Seed size	39.14	> 3	mm
			Dispersal agent	34.26	Birds	
			LDMC	12.03	< 357	mg/g
			Bark thickness	7.52	> 3.25	mm
			SLA	4.74	< 78	mm^2/g
			Maximum height	2.31	< 10.5	m
Survival	0.50	0.34	Dispersal agent	39.5	all	
			Maximum height	34.14	< 11.3	m
			Seed size	26.36	> 3.6	mm
Relative growth rate	0.38	0.15	Dispersal agent	42.58	Birds and wind	
			Seed size	23.3	< 5.3	mm
			LDMC	16.25	< 359	mg/g
			SSD	12.53	> 0.57	g/cm^3
			LA	5.34	> 47	mm^2

Which species are likely to overcome the filters imposed by bracken?

After applying the trait threshold filters to a larger dataset containing 46 species, the species with the highest active restoration values were: *Hieronyma* sp. nov., *Clusia trochiformis, Palicourea reticulata, Hedyosmum angustifolium, Hieronyma fendleri*, *C.*

elongata, C. lechleri, Myrcia splendens, Ocotea puberula and *Clusia* sp. nov. (Table S5). Notably, all of these species are bird-dispersed.

When the filters were applied to a dataset of 95 common species in our study area, with six traits, the species with the highest active restoration values were: *Geissanthus ambigua, Clusia trochiformis, Persea bilocularis, Hieronyma fendleri*, *Myrsine latifolia, Prunus guanaiensis, P. pleiantha, Coussarea rudgeoides, Palicourea flavifolia* and *Palicourea tristis* (Table S6). The best species in our smaller dataset were also included among the 30 best species in the larger dataset. Consistently, all of them are bird-dispersed.

Are the species with the highest probabilities of overcoming the filters abundant in old-growth forests?

We did not find a significant relationship between the active restoration values and the abundance of the species in old-growth forests ($R^2 < 0.028$, Fig. 2).

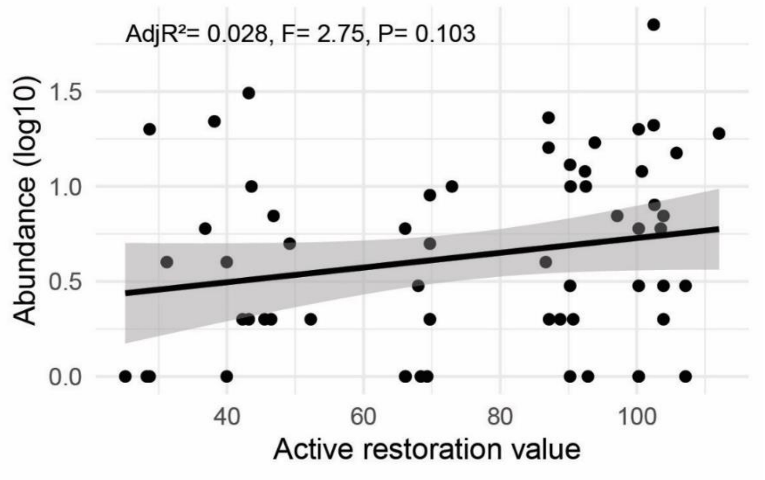

Fig. 2. Simple regressions between the active restoration values obtained in this study for 95 species and the abundance (transformed to log10+1) of the same species in plots set in old-growth forests from our study area (data extracted from Lippok et al. 2014).

4. Discussion

Our findings reveal that specific functional traits are linked to successful seed germination, seedling survival and growth in bracken-dominated areas. The dominant traits determining success were dispersal agent, seed size and maximum tree height. Our results highlight the importance of seed-dispersing birds as vectors carrying forest seeds to bracken-dominated areas, as well as large seeds for successful germination and survival, and short-stature trees for seedling survival. Overall, conservative traits such as low specific leaf area, high stem-specific density, large seed size, short adult-stature and thick bark were favored. The high predictive power of our approach suggests that our model can be used as a blueprint to select species for ecological restoration projects in other tropical bracken-dominated areas with a distinct species pool.

All species that were able to surpass the filters were dispersed by birds. Although 71% of individuals in reference forest plots are dispersed by birds (cf. Missouri Botanical Garden – Bolivia Program, 2024), only 8.4% of the individuals naturally recruiting in the bracken-dominated areas are tree species dispersed by birds (López et al., 2024). However, these species comprise 73% of the tree species registered naturally recruiting in bracken-dominated areas (López et al., 2024). These patterns may be attributed to dispersal limitation as the main limiting factor hindering forest regeneration in bracken-dominated areas (Gallegos et al., 2016, 2024; Mayta et al., 2024), reflected by the low density of animal-dispersed tree species. Hence, their presence in a relatively high species richness indicates their capacity to recruit in these deforested areas after the limited seed dispersal.

Seed size was positively related to seed germination and seedling survival but negatively related to RGR, reflecting the growth-survival trade-off (Rüger et al., 2018). This pattern, reported in several studies (e.g., Gibert et al., 2016; Poorter et al., 2008), could explain why forest regeneration in bracken-dominated areas is slow, as most species that are able to germinate and survive there have low growth rates. In general, seedlings from large-seeded species have higher germination and survival rates than those from small-seeded species (Baraloto et al., 2005; Visser et al., 2016), higher stress tolerance (Muller-Landau, 2010), higher competitive ability (Leishman, 2001), higher tolerance to thick litter layers (Facelli & Pickett, 1991), and species that establish under shade tend to have larger seeds (Leishman et al., 2000). The advantage of large-seeded species could be also associated with their high energy and nutrient contents and the production of seedlings with thicker and denser leaves and roots, with high survival rate and slow growth (Metz et al., 2023). Germination and survival were higher for short-statured trees that reproduce at a smaller size, have shorter generation times, exhibit greater drought resistance than tall trees and have high a production of recruits (Fajardo et al., 2019; Rüger et al., 2018).

Other trait filters acting in bracken-dominated areas are related to the shading effect of bracken, which selects for species with traits associated with shade-tolerance and conservative life history strategies, such as low specific leaf area (SLA), high stem-specific density (SSD) and wood density, large seed size, short adult-stature and thick bark (Niinemets, 2006; Wright et al., 2010). Conversely, traits associated with acquisitive strategies, such as low leaf dry matter content (LDMC) and high leaf area (LA), were favored for relative growth rate (RGR).

Although we used adult leaf traits to predict seedling performance, as done in some previous studies (Lasky et al., 2015; Visser et al., 2016), various factors contributed to the strong predictive power of traits. First, we found a relatively high correlation between the adult traits and seedling leaf traits in our study area (Pearson's *r* =0.67 to 0.96 for saplings-adults, *r* = 0.34 to 0.61 for seedlings-adults, and *r* = 0.25 to 0.79 for seedlings-saplings, C. Lopez unpublished data), suggesting that the traits we used are representative from the seedling stage. Second, there is a strong correlation between seedling SLA and SSD with seed mass in different tropical forests (Metz et al., 2023), and a high correlation between our seed mass and seed size traits. By incorporating seed size in our analyses, we indirectly accounted for the effects of seedling's SLA and SSD, and directly those of adult's SLA and SSD. Third, although the effects of traits on demography may change through ontogeny, the seedling stage is determinant for plant establishment because the regeneration phase is the main bottleneck during life-cycle (Iida et al., 2014; Poorter, 2007). Therefore, the traits favored in bracken-dominated areas that we detected in the early life stage must be determinant for tree establishment and forest succession.

After applying the filters to two larger datasets, species with the highest establishment probabilities were *Geissanthus ambigua, Clusia trochiformis, Persea bilocularis, Hieronyma fendleri* and *Myrsine latifolia*. Most of the species favored in our study were observed in bracken-dominated areas during advanced stages of succession, and some, such as *C. trochiformis, Hieronyma fendleri, Hedyosmum racemosum, Palicourea tristis* and *Myrsine* spp., are frequently found in secondary forests. However, due to the high seed limitation in bracken-dominated areas (see below), many of the selected species were found in low densities in old-growth forests (Lippok et al., 2014), and we did not find a positive relation between the active restoration value and species abundance . These results suggest that the abundance of tree species in the old-growth forest should not be considered as a reference to guide plant species selection in restoration projects, at least in bracken-dominated areas, because they might not be adapted to overcome the filters for seedling establishment. Species selection for restoration projects should target traits that optimize plant fitness and focus on the species with the highest probabilities of establishment (Laughlin, 2014), to justify the economical investment. Other studies in bracken-dominated areas have suggested transplanting shrubs or the direct seed addition and seedling transplant of late-successional/shade-tolerant/large seeded species (Gallegos et al., 2015, 2016; López et al., 2024; Saavedra et al., 2015). Our results align with these suggestions and contribute in a more specific way to the species selection, by highlighting the importance of short-statured trees and bird-dispersed species.

Arrested forest succession in bracken-dominated areas is associated with seed limitation (Gallegos et al., 2016; Mayta et al., 2024; Ssali et al., 2017). Here we detected that this limitation is probably exacerbated by the fact that the species favored by bracken are dispersed by birds and have large seeds. Consequently, to increase seed dispersal and to promote plant-animal interactions (Ladouceur et al., 2022), the inclusion of animal attractants and food resources for forest birds is urgently needed. Accordingly, perch structures showed a potential to reduce seed limitation in bracken-dominated areas, by increasing tree seed density and richness, 200 and 22 times, respectively, and seedling density and richness, 16 and 8 times, respectively (Mayta et al., 2024). This restoration strategy should be accompanied by the direct seed addition and seedling transplant of bird-dispersed species of short-statured trees, preferentially with large seeds.

Given the increase in fires in the tropical region, mainly related to warmer and drier conditions caused by climate change, bracken-dominated areas are increasing at an alarming rate (Velazco et al., 2024). Therefore, active restoration projects are needed to promote forest succession. We expect that our approach will be useful in other tropical areas dominated by bracken to inform such projects. Our approach also highlights the importance of seed addition experiments, especially in areas under dispersal limitation, to study the performance of different species under natural conditions. These approaches are valuable for identifying the traits that enhance the performance of certain species under specific conditions and can be used to design a seed or planting mix for a restoration project by selecting species with the highest establishment probabilities (Laughlin, 2014). Trait-based quantitative frameworks could be a powerful tool to select native species to optimize restoration strategies (Carlucci et al., 2020; Fremout et al., 2022).

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Chapter VI. Comparison of seed addition and seedling planting for the restoration of bracken-dominated areas under different management methods

This paper is ready to submission as

López, C. L., Mayta, C., Hensen, I. & Gallegos, S. C. Comparison of seed addition and seedling planting for the restoration of bracken-dominated areas under different management methods.

Abstract

The dominance of bracken fern (*Pteridium esculentum* subsp. *arachnoideum*) in fire-disturbed tropical forests is a major barrier to their natural regeneration and requires active restoration measures. This study compares the effectiveness of two restoration techniques: seed addition and seedling planting. The recruitment success and growth of 11 animal-dispersed tree species are examined after three years under different bracken management strategies using the following treatments: (a) fronds and litter intact (F+L+); (b) fronds intact and litter removed (F+L-); (c) fronds removed and litter intact (F-L+); and (d) fronds and litter removed (F-L-). Our questions were: (i) How do recruitment success and growth rates of tree species respond to different bracken management strategies? and (ii) Which functional traits are associated with better seedling performance under different bracken management treatments. Seedling planting significantly outperformed seed addition and showed higher recruitment success and relative growth rates for all treatments. Recruitment success was 27% and 26.8% higher for seedling planting in F+L+ and F+L-, respectively. For F-L+ and F-L-, recruitment rates of planting seedlings were 23% and 28.8% higher, respectively. Relative growth rates followed the same pattern, with the highest values in F+L+, where seedling planting performed 2.1 times better than seed addition, followed by F+L- where the values were 1.52 times higher. Species with larger seeds, larger leaf area, and higher specific leaf area performed better under bracken. Of all the traits assessed, larger seed size, leaf area and specific leaf area were related to species with a better performance under bracken. Contrary to common and widespread assumptions, the complete removal of bracken fronds and litter resulted in lower recruitment rates for both techniques, suggesting that intact bracken can provide a protective microenvironment for seedlings. While seedling planting had a stronger overall response, seed addition showed potential for species with traits favoring early establishment. Our findings suggest that integrating both techniques, with an emphasis on stress-tolerant, animal-dispersed species with large seeds, greater leaf area, and higher leaf dry matter content, could optimize restoration efforts in bracken-dominated environments.

Keywords: active restoration, direct seeding, functional traits, *Pteridium*, transplanting.

Introduction

Andean tropical montane forests are among the most biodiverse ecosystems in the world (Myers et al., 2000). They harbor an extremely diverse and unique flora and fauna, with many species restricted to the mountains (Pillay et al., 2022; Rahbek et al., 2019). However, these forests are increasingly threatened, mainly due to anthropogenic disturbances such as land use changes and fire, which alter their composition and functionality (Aguilar-Garavito et al., 2021; Oliveras et al., 2014). Fire, in particular, has become a recurrent disturbance, resulting in extensive deforested and degraded areas (Aguilar-Garavito et al., 2021; Laurance et al., 2012; Oliveras et al., 2018), often resulting in the long-term dominance of bracken fern (*Pteridium* spp.) (Marrs et al., 2000). Bracken is an highly competitive pioneer species that thrives in disturbed environments (Le Duc et al., 2007; Roos et al., 2010). Its success is mainly attributed to its dense fronds and the accumulation of a deep litter layer, which create a shaded environment that hinders the establishment and growth of other species, particularly early-successional trees (López et al., 2024; Ssali et al., 2019; Toledo-Aceves et al., 2022). Consequently, natural forest succession in bracken-dominated areas is typically slow, because the tree species able to establish in these environments (i.e. mid-, late-successional species) (López et al., 2024; Ssali et al., 2019; Toledo-Aceves et al., 2022) face significant seed dispersal limitation (Gallegos et al., 2016; Münzbergová & Herben, 2005). This limitation is exacerbated by the lower abundance and different composition of seed-dispersing animals in bracken-dominated areas, leading to reduced tree recruitment (Gallegos et al., 2024; Saavedra et al., 2015), which further delays forest regeneration (Carvalho et al., 2022; Hartig & Beck, 2003; Roos et al., 2010).

Therefore, to overcome these constrains, active restoration strategies have been proposed to accelerate forest recovery. One proposed strategy involves reducing bracken cover through repeated annual cutting and regular application of herbicides (Ghorbani et al., 2006; Pakeman et al., 2002). However, this method is cost-effective only in the short-term (Pakeman et al., 2000), as bracken often regrows rapidly (Marrs et al., 1998). Moreover, such strategies are unlikely to be widely adopted as they require substantial financial and human resources (Douterlungne et al., 2013). An alternative approach should consider the ecological dynamics of bracken-dominated areas, recognizing that bracken modifies micro-environmental conditions in ways that may favor shade-tolerant plants (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2019). Although previous research in these ecosystems has focused on the effects of bracken on natural recruitment and on few early- and late-successional species (López et al., 2024; Ssali et al., 2019), little is known about the effects of bracken fronds and litter on the development of animal-dispersed species and other traits which can be related with recruitment success in this environments.

Functional traits are indicators of ecological strategies (Visser et al., 2016; Wright et al., 2007) and can help to predict species responses to environmental constrains (Metz et al., 2023). For example, seed size is the strongest predictor of initial seedling growth, but as seedlings transition to autotrophic growth, other traits such as leaf mass per unit area (LMA) become more important (Poorter et al., 2008). Other leaf traits such as leaf area (LA, in cm^2), specific leaf area (SLA, in cm^2/g), and leaf dry matter content (LDMC, in mg/g) provide valuable insights into species resource-use strategies, growth potential, and stress tolerance (Poorter & Bongers, 2006), which are key factors for successful establishment in degraded environments. To identify the most suitable species for planting, short-term screening of growth and survival rates may be needed to ensure their resilience in these challenging conditions (Martínez-Garza et al., 2013). Techniques such as seed addition and seedling planting offer promising solutions for enhancing plant density and diversity (Douterlungne et al., 2010; Palomeque et al., 2017; Slocum et al., 2006; Toledo-Aceves et al., 2022) and overcome dispersal limitation. Seed addition increases the availability of propagules at sites where natural seed rain is scarce, while seedling planting reduces mortality in early-stages and improves recruitment success (Holl & Aide, 2011; Khurana & Singh, 2001). Despite their potential, the effectiveness of these techniques remains context-dependent, as bracken-dominated areas exhibit multiple abiotic (i.e., light, temperature, humidity) and biotic (i.e., competition, allelopathy) filters, suggesting that a combination of functional traits approach is needed to ensure seedling establishment and early growth performance.

To determine the most effective strategy for restoring bracken-dominated areas, we conducted a field experiment to evaluate different bracken management approaches and sowing techniques. Because bracken modifies micro-environmental conditions and affects tree recruitment (López et al., 2024), we tested whether the removal of bracken fronds and litter, combined with seed addition and seedling planting, could promote early recruitment and growth. Since functional traits influence species responses to environmental filters, we also examined which traits are associated with improved seedling performance under different bracken management strategies. In particular, we addressed the following questions: (i) How do recruitment success and growth rates of tree species respond to different bracken management strategies (removal of bracken fronds and litter) and restoration techniques (seed addition and seedling planting)? and (ii) Which functional traits are associated with better performance of seedlings under different bracken management treatments?

Materials and methods

Study area

The study was conducted between 2019 and 2023 on the eastern slope of the Andes near the towns Chulumani and Irupana in the province of Sud Yungas, La Paz, Bolivia (16º24’37” S, 67º31’37” W and 16º27’24” S, 67º25’50” W), between 1.850 and 2.300 m asl. The forest is classified as tropical montane humid forest, with a mean annual temperature of 19.5°C and a mean annual precipitation of 1440 mm (Beck et al., 2024). Frequent uncontrolled anthropogenic fires and the expansion of *Erythroxylum coca* plantations have led to severe forest fragmentation (Killeen et al., 2005, 2008). As a result, the landscape consists of two large remnants of continuous old forest, covering approximately 4000 and 2000 ha, respectively, surrounded by extensive areas dominated by bracken fern (*Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) J. A. Thomson) and shrubs from the Asteraceae, Ericaceae and Melastomataceae families (Beck et al., 2024; Lippok, Walter, et al., 2013). At forest edges, the most common tree species include *Hedyosmum racemosum* (Chloranthaceae), *Clusia trochiformis* (Clusiaceae), and *Hieronyma fendleri* (Phyllanthaceae), while species from the Rubiaceae, Piperaceae, Melastomataceae, and Lauraceae families are more abundant in the forest interior (Beck et al., 2024; Lippok et al., 2014). Most woody plant species are dispersed primarily by birds and bats (Lippok et al., 2014), although terrestrial mammals such as *Mazama americana* and *Dasyprocta variegata* can also contribute to seed dispersal (Gallegos et al., 2024).

Experimental design

At eight study sites, which were at least 1 km apart and had been last burned between 5-15 years prior to the study, we established 50 x 50 m plots in bracken-dominated areas approximately 100 m from the forest edge (Fig. S1). Each plot was divided into four 25 x 25 m subplots, in which the following treatments were applied: 1) fronds and litter intact (F+L+); 2) fronds intact and litter removed (F+L-); 3) fronds removed and litter intact (F-L+); and 4) both fronds and litter removed (F-L-) (Fig. 1a,b). To maintain treatments, fronds were carefully cut with a machete at ground level every four months and litter was removed manually.

Seed addition and seedling planting

Based on fruit availability, we selected 11 tree species commonly found in our study area in the forest interior and/or at the forests edges (Beck et al., 2024) (Table 1). We included species representing a broad range of functional traits (e.g. seed size, leaf area, specific leaf area, leaf dry matter content) (Palma & Laurance, 2015). Fruits were collected from at least ten individuals per species, mixed, and seeds were manually cleaned and counted before sowing. Since all selected species produce fleshy fruits, seeds were collected two days before sowing at each of the eight sites and stored in small flasks with damp paper to maintain moisture. In each subplot, nine rows were carefully delineated to minimize bracken disturbance (Fig. 1b). Four rows were designated for the seed addition experiment. Within each row, four 1x1 m2 quadrats were established and further divided into four 50 x 50 cm2 sub-quadrats, leaving the lower right sub-quadrant unsown to facilitate the evaluation. The squares were spaced 2 m vertically and 3 m horizontally, with a path between rows to facilitate measurement (Fig. 1b). Species were randomly assigned to the sub-squares, with four subsamples in each treatment. Seeds were sown at different densities according to their seed size, which is assumed to be negatively related to seed production and positively related to seedling performance (Leishman, 2001; Visser et al., 2016). Seeds were dropped to simulate natural dispersal.

Table 1. List of the species included in the study and number of seeds sown per sub-square in the seed addition experiment.

Family	**Species**	**Seed size (SS)**	**# of seeds sown**
Hypericaceae	*Vismia rusbyi* Ewan	1.8	15
Hypericaceae	*Vismia crassa* (Rusby) Blake	2	15
Piperaceae	*Piper bolivianum* C. DC.	2.6	20
Chlorantaceae	*Hedyosmum racemosum* (Ruiz & Pav.) G. Don	2.8	15
Clusiaceae	*Clusia elongata* Rusby	4.8	10
Clusiaceae	*Clusia lechleri* Rusby	5.1	10
Rhamnaceae	*Frangula sphaerosperma* (Sw.) Kartesz & Gandhi	5.4	10
Clusiaceae	*Clusia* sp.	5.7	10
Clusiaceae	*Clusia trochiformis* Vesque	6.1	10
Lauraceae	*Aiouea montana* (Sw.) R. Rohde	11.1	3
Symplocaceae	*Symplocos arechea* L´Herit.	15.3	3

At the same time, seeds from the same cohort were sown in a tree nursery at the Biological Station Santiago de Chirca (16º23’50.23” S, 67º34’53.53” W, 2080 m asl) under a 50% shade mesh with regular irrigation and grown in separate bags from 1l each for one year. The nursery-raised seedlings were then planted into the plots in alternating rows with the seed addition experiment (Figure 1b). Both experiments were started during the rainy season (November - February) to promote germination and survival (Paterno et al., 2016). Measurements for the seed addition experiment were conducted at 6, 12, 24 and 36 months, with a focus on the cumulative outcome at 36 months. For transplanted seedlings, the first assessment of height took place immediately after planting, with subsequent assessments of seedling growth and survival at 24 and 36 months.

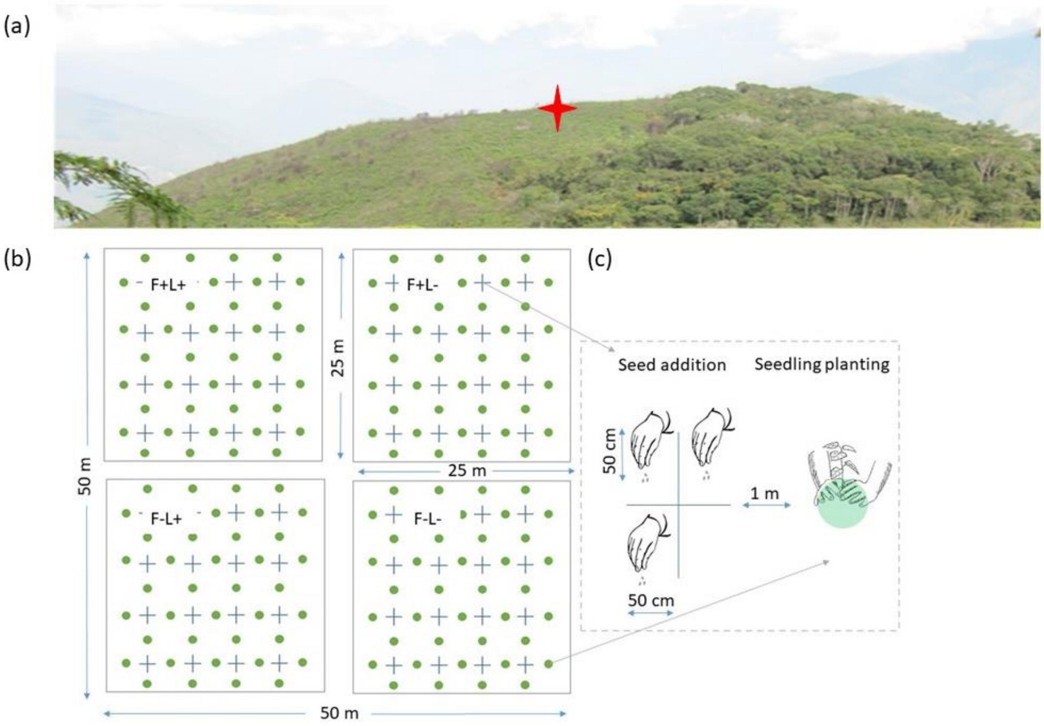

Fig. 1. Experimental design for the seed addition and seedling planting experiments with 11 species. (a) Photograph of a bracken-dominated area in which the subplots representing different sites were established (n= 8). (b) Overview of the plots and subplots for the treatments: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. (c) Detail of the seed addition and seedling planting experiments: blue crosses represent squares in which three species were sown, and green circles represent seedlings of the same cohort transplanted one year after being nursery-raised, alternating with the rows with sown seeds.

Trait measurements

After 36 months, at the end of the experiment, we harvested one leaf from all seedlings survived from the two experiments on seed addition and seedling planting. We measured three functional traits: leaf area (LA, in cm2), specific leaf area (SLA, in cm2/g) and leaf dry matter content (LDMC, in mg/g). Additionally, we considered the seed size of each species (SS, in mm). All traits were measured following standardized protocols (Pérez-Harguindeguy et al., 2013).

Data analysis

For both seed addition and seedling planting experiments, recruitment success was determined as the proportion of individuals that survived until the final assessment (i.e., after 36 months) (Paterno et al., 2016; Barczyk et al., 2024). Relative growth rate (RGR) was calculated using the formula $(\ln(h_t+1) - \ln(h_t))/t$, where h is the individual height in cm at time *t* and *t*+1, and t is the time in days between measurements.

To compare seedling performance from seed addition and seedling planting in the four bracken management treatments, we used generalized linear mixed-effects models (GLMMs), with recruitment success and RGR as response variables. Recruitment success was modeled using a beta-binomial error distribution to account for over-dispersion (Crawley, 2012), while RGR was modeled with a Gaussian distribution. Bracken treatment (presence or absence of fronds and litter), restoration technique (seed addition vs. seedling planting) and their interaction were included as fixed effects, while site and species were included as random effects. Similar models were performed for each of the 11 species separately, with site used as a random effect. All models were fitted using the 'glmmTMB' package (Brooks et al., 2017), and each model was validated by analyzing residuals in the 'DHARMa' package (Hartig, 2022). *Post hoc* Tukey tests among treatments were conducted using the 'emmeans' package, and all figures were created using the 'ggplot2' package.

To quantify the influence of functional traits on recruitment success and growth in different bracken management treatments, we performed a Redundancy analysis (RDA) (Kleyer et al., 2012) using the function rda() from the vegan package (Oksanen et al., 2018). Significance of the constrained ordination models was assessed using a Monte Carlo permutation test based on 9999 permutations. To account for multicollinearity among the functional traits, we calculated variance inflation factors (VIF) and maintained those with VIF values <10 (Zuur et al., 2010), leaving all four traits in the models. (R Core Team, 2024).

Results

In the seed addition experiment, a total of 3388 seeds were sown, of which 1497 (44.2%) germinated. Of these seedlings, 720 (48.1%) successfully recruited after three years. In the seedling planting experiment, a total of 949 seedlings were planted, of which 714 (75.2%) successfully recruited.

Recruitment success was significantly higher for seedling planting compared to seed addition across all bracken management treatments (Fig. 2a, Table S1). In the F+L+

treatment, recruitment success was 27% greater for seedling planting than for seed addition. Similarly, in the F+L- treatment, seedling planting outperformed seed addition, with recruitment success being 26.8% higher. Significant differences were also observed in the F-L+ and F-L- treatments, where recruitment success was 23% and 28.8% higher, respectively, when seedling were planted than when seeds were added. We found similar trends in the 11 species studied (Fig. S2, Table S2).

Relative growth rates (RGR) followed a similar pattern, with seedling planting consistently outperforming seed addition in most treatments (Fig. 2b). The highest relative growth rate was observed in the F+L+ treatment for seedling planting, which was 2.1 times higher than that achieved with seed addition, followed by the F+L- treatment, in which RGR was 1.52 times higher for seedling planting than seed addition. In contrast, no significant differences were found in the growth of seedlings from seed addition among bracken management treatments, nor in the growth of transplanted seedlings in the treatments without bracken fronds (F-L+ and F-L-) compared to those from seed addition. Each species responded differently to bracken management and restoration technique in terms of RGR (Fig. S3, Table S3).

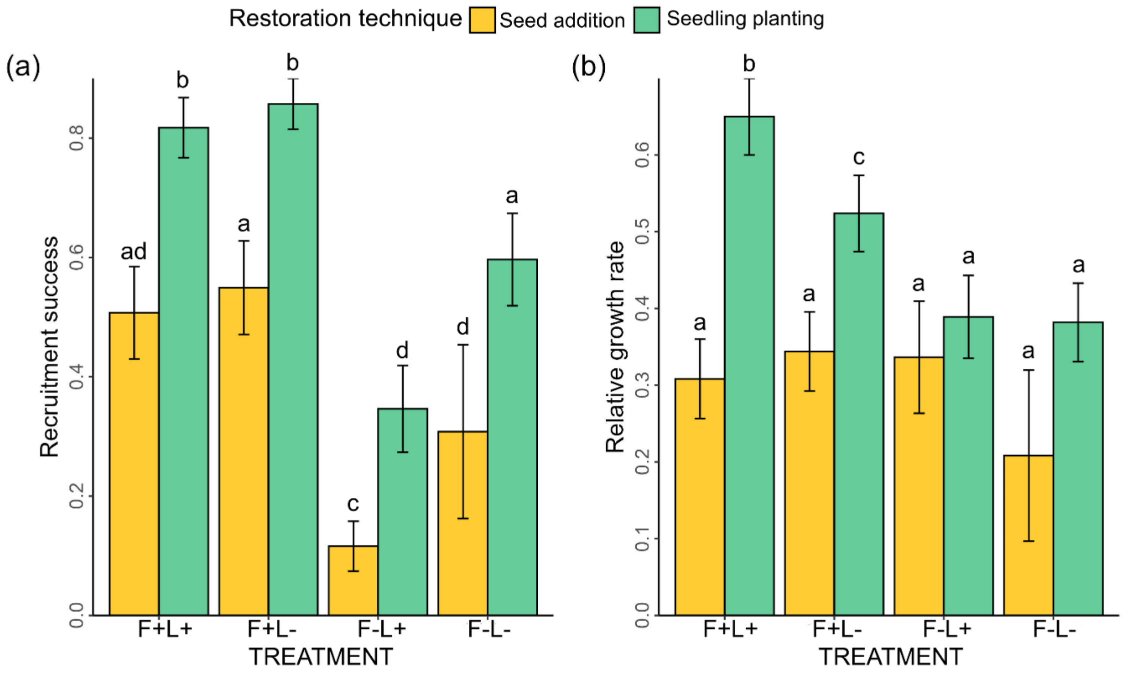

Fig. 2. Proportion of recruitment success (a) and relative growth rate (b) at 36 months, according to seed restoration technique in experimental bracken treatments: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots represent the predicted values from the generalized linear mixed-effects models (GLMMs) ± SE. Different lowercase letters indicate significant differences at the 0.05 level based on *post hoc* Tukey tests.

Redundancy analysis (RDA) illustrates the correlation among four functional traits of all species and the bracken management treatments (Figs. 3 and 4). The functional traits significantly explained the recruitment success found in the different bracken management treatments for seed addition (F = 2.44 p = 0.003, Fig. 3a). The first two axes together explained 88.9% of the variance, but only the first axis, which explained 72.57%, was significant (F = 7.11 p = 0.002). Along the first axis, treatments with bracken fronds present (F+L+, F+L-) were positioned on the left side, where species such as *Clusia trochiformis*, *Clusia sp*. and *Symplocos arechea*, which showed the highest recruitment success, were positively related to SLA and LA, and, to a lesser extent, to LDMC and SS. Functional traits significantly explained recruitment success in the different management treatments for seedling planting (F = 4.27, p < 0.001, Fig. 3b), with the first two axes accounting for 66.7% of the variance. However, only the first axis, which explained 42.1% of the variance, was statistically significant (F = 11.85, p = 0.001). Along this axis, treatments with bracken fronds (F+L+, F+L-) were positioned on the right side and were positively related to SS and SLA and negatively related to LDMC (Fig. 3b).

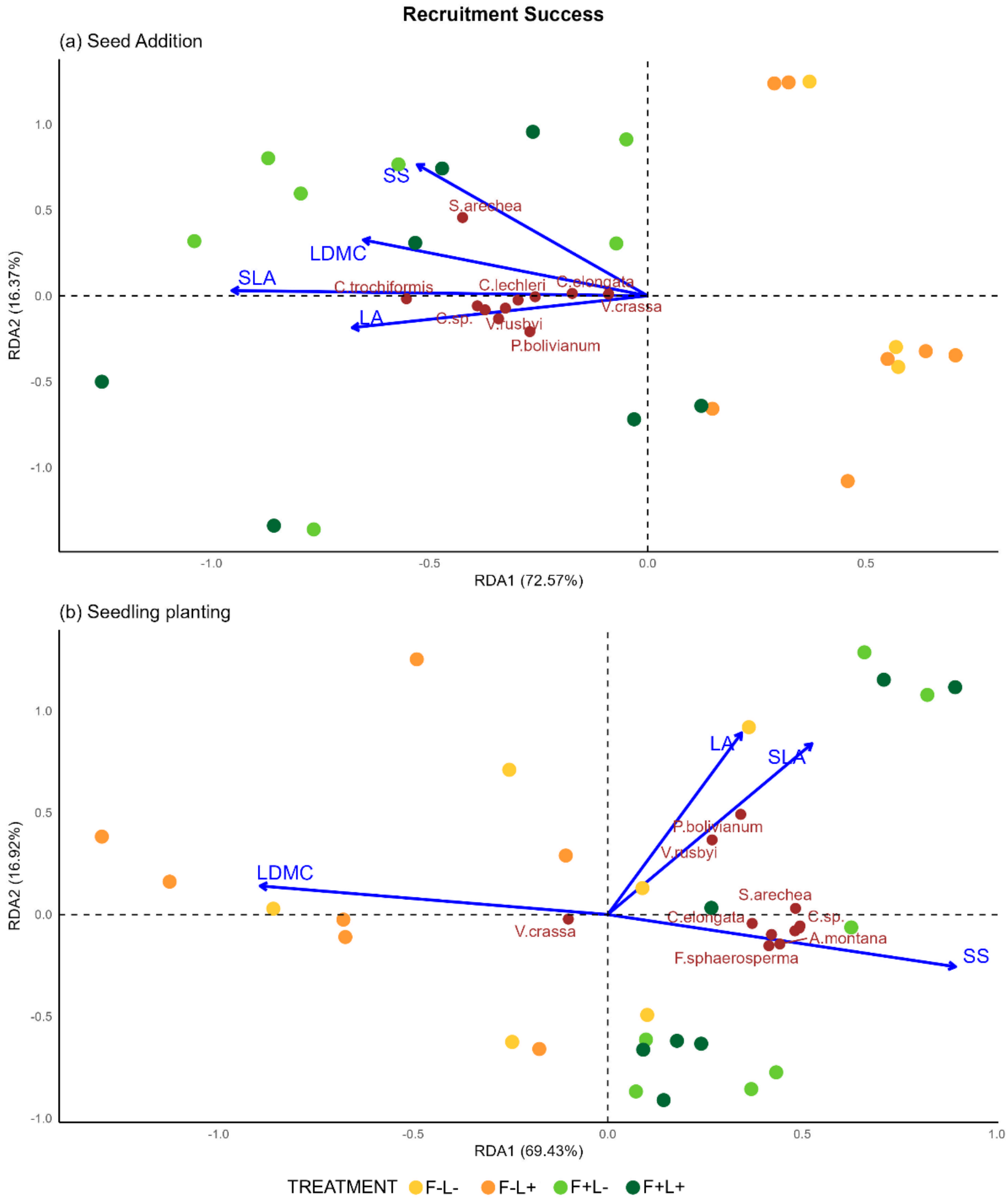

Fig. 3. Redundancy Analysis (RDA) ordination of weighted means of trait values for each bracken management treatment based on 36-months recruitment success of 11 tree species using different restoration techniques: (a) seed addition and (b) nursery-raised seedling planting. Blue arrows: functional traits; dots: subplots with different bracken treatments; red letters: species (full names can be found in Table 1).

Functional traits significantly explained RGR after seed addition (F = 2.206, p = 0.01, Fig. 4a). The first two axes of the model accounted for 89.5% of the variance, with only the first axis, which explained 77.6%, being statistically significant (F = 6.85, p = 0.004). Functional traits also significantly explained RGR in the seedling planting experiment (F = 2.96, p < 0.001, Fig. 4b). The first two axes represent 84.7% of the total variance, but only the first axis, which explains 69.2%, was significant (F = 8.21, p = 0.003). Relative growth rate after seed addition and seedling planting showed the same trend than recruitment success. In the seed addition experiment, treatments with bracken fronds (F+L+, F+L-) were positively associated with SLA, SS and LDMC, while in the seedling planting experiment, both treatments with fronds were positively related to species with higher SS and SLA but lower LDMC.

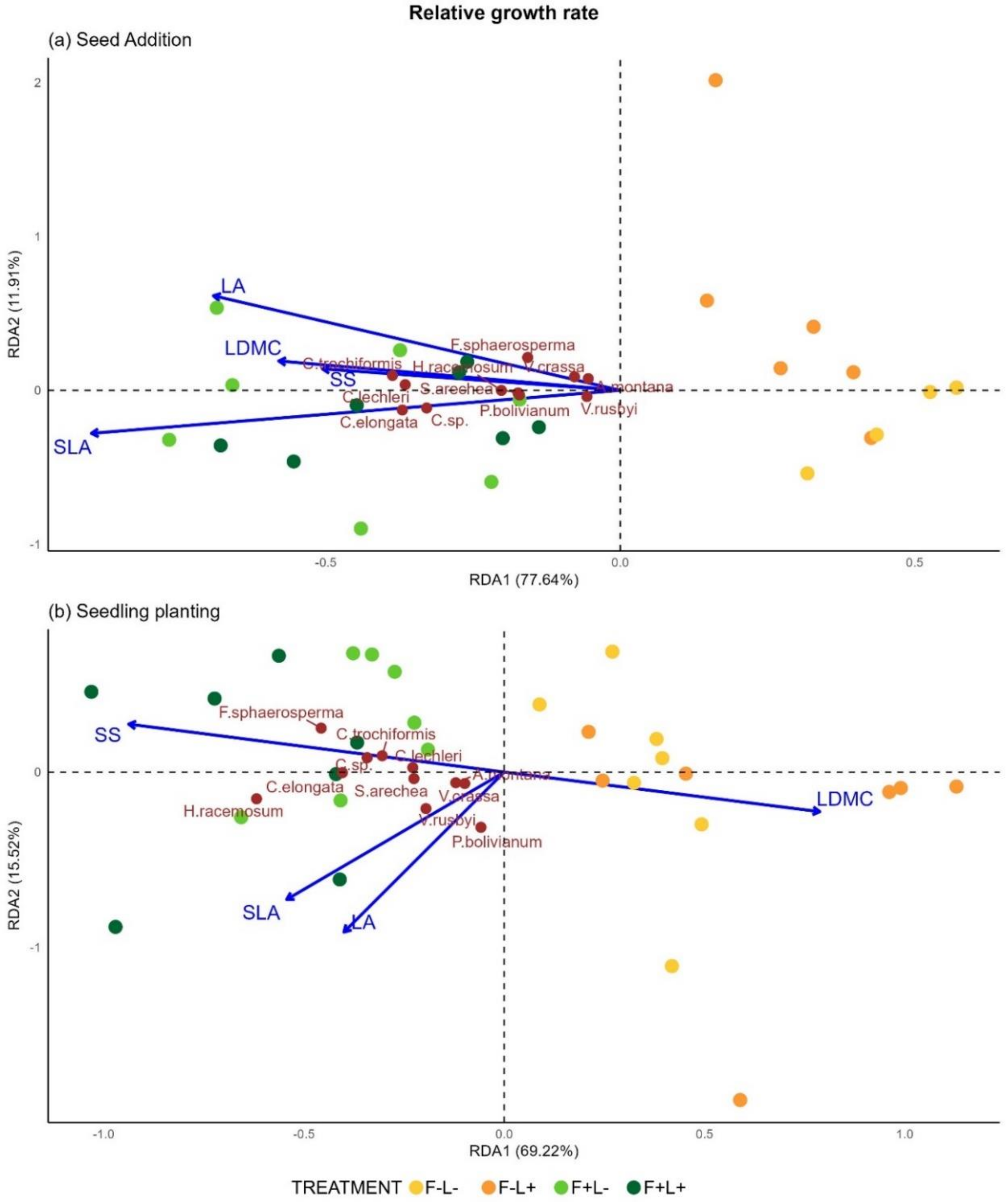

Fig. 4. Redundancy Analysis (RDA) ordination show the weighted mean trait values for each bracken management treatment, based on RGR of 11 tree species using different restoration techniques: (a) seed addition and (b) seedling planting, after 36 months. Blue arrows: functional traits; dots: subplots with different bracken treatments; red letters: species (full names can be found in Table 1).

Discussion

We examined the performance of 11 tree species under different strategies for managing bracken, comparing two restoration techniques: seed addition and seedling planting. Seedling planting resulted in higher recruitment success and higher relative growth rates for the different bracken management treatments compared to seed addition. These results indicate that under natural conditions, there is an important filter during the first years of seedling recruitment in bracken-dominated areas. For both restoration techniques, frond removal generally resulted in lower recruitment success and growth. Additionally, we found a significant relationship between functional traits and species performance for each bracken-management treatment, highlighting the importance of considering species functional strategies and planting techniques when selecting candidates for restoration in bracken-dominated areas.

Several studies examined the relative success of restoration techniques such as seed addition or seedling planting, each of which has its own advantages and limitations (Palma & Laurance, 2015). Seedling planting is widely used due to higher establishment success, especially in degraded environments with strong environmental filters (Holl et al., 2011). However, it is a resource-intensive technique that requires propagation in nurseries, transportation and planting which limits its scalability (Douterlungne et al., 2010; Zahawi & Holl, 2009). In contrast, seed addition offers a more cost-effective alternative for large-scale restoration (Bonilla-Moheno & Holl, 2010; Douterlungne et al., 2010), although its success is highly dependent on seed availability, predation, and microsite conditions (Eriksson & Ehrlén, 1992; Ssali et al., 2018).

All 11 species in our study are animal-dispersed and showed a recruitment between 20% and 80% for seed addition and between 70% and 100% for seedling planting, after three years. The high recruitment success after seed addition observed in most species in our study provides further evidence that these ecosystems are not saturated with propagules but instead are subject to strong dispersal limitation (Münzbergová & Herben, 2005), which is a critical bottleneck in bracken-dominated areas (Gallegos et al., 2016). This suggests that active restoration is needed to overcome this limitation. The higher recruitment success observed in seedling planting compared to seed addition can be attributed to the advantages of nursery propagation. Due to controlled conditions (i.e., frequent watering, independent pots, etc.), nursery-raised seedlings develop greater above- and below-ground biomass with an accumulation of reserves, which improves their establishment potential after transplanting (Holl et al., 2011; Zahawi & Holl, 2014). In contrast, direct seeding in bracken-dominated areas faces several constraints on initial seedling establishment, including mechanical barriers from a deep litter layer (Ghorbani et al., 2006), recruitment limitation by predation (Ssali et al., 2018), water stress during dry season, low nutrient content (Lippok, Beck, et al., 2013), and density-dependent intra and interspecific competition (Ramula & Buckley, 2009).

The control of bracken remains a major challenge in tropical forest restoration (Levy-Tacher & Morón-Ríos, 2023). While previous studies suggest that combining mechanical control and tree planting is an effective strategy to promote forest recovery (Xavier et al., 2019, 2023), our results highlight the complexity of the role of bracken in regeneration dynamics. Contrary to the widespread expectation that removal of bracken would enhance tree recruitment, we found that complete removal of both fronds and litter led to lower recruitment for both seed addition and seedling planting. Previous findings showed that bracken fronds and litter can create favorable micro-environmental conditions by reducing photosynthetically active radiation, reducing soil temperature and increasing soil moisture, thereby promoting tree recruitment (López et al., 2024). Additionally, the presence of bracken might indirectly benefit seedlings by reducing competition with grasses, minimizing desiccation or providing some protection from herbives (Azevedo-Schmidt et al., 2024). We observed that relative growth rates were also lower in treatments where fronds and litter were removed, suggesting that early seedling development may depend more on microclimatic stability (López et al., 2024). We suggest that selecting for a range of species with traits that benefit from bracken presence could reduce or even eliminate the need for bracken control.

Species with traits favoring early establishment, such as large seed size and stress tolerance, perform better after seed addition (Cole et al., 2011; López et al., 2024; Ssali et al., 2019; Toledo-Aceves et al., 2022). Accordingly, the lowest recruitment by seed addition was mainly observed in the three smallest-seeded species of our set, belonging to *Vismia* and *Piper,* two genera typical of pioneer and bat-dispersed species, respectively (Ferreira et al., 2024; Pearson et al., 2002). This result is consistent with previous findings in the study area, where seedling establishment of these species is reduced under bracken (Mayta et al., 2024), and where seed size played a significant role in recruitment success (López et al., in prep.). In our study, we found that functional traits such as high leaf area (LA) and specific leaf area (SLA), which are related to light acquisition and photosynthetic efficiency, and seed size (SS), a trait associated with initial establishment and competitive abilities (Milberg et al., 2000; Moles & Westoby, 2004; Poorter et al., 2008), were positively associated with seedling recruitment and growth under treatments where bracken fronds were present. These traits were favored for both seed addition and seedling planting techniques. In contrast, high leaf dry matter content (LDMC), a trait typically associated with resource conservation and drought tolerance (Hodgson et al., 2011), was positively associated with seedling recruitment and growth after seed addition, but negatively associated with these processes after seedling planting. This difference may be related to the filters present in bracken-dominated areas during early development, when species with conservative traits to tolerate stress have an advantage. On the other hand, improved performance of species with low LDMC in the presence of bracken after seedling planting suggests that these seedlings have already overcome initial stress from bracken fronds and litter. This is consistent with higher performance of species with high LDMC after bracken removal, for which stress tolerance is essential for survival in harsh environments (Gallegos et al., 2015; López et al., 2024). These findings highlight the importance of selecting species with functional traits that enhance survival under site-specific conditions (Martínez-garza et al., 2013), particularly when designing restoration strategies in areas dominated by bracken.

Given the increasing prevalence of bracken-dominated landscapes due to fires and land-use change, active restoration efforts are urgently needed (Velazco et al., 2024). Our study suggests that while seedling planting achieved better performance in bracken-dominated areas, the results of seed addition indicate its potential as a viable strategy for species with traits favoring early establishment. Integrating both techniques, with a focus on stress-tolerant, animal-dispersed species with higher seed size, leaf area and leaf dry matter content, could optimize restoration efforts in these challenging environments. Seed dispersal is another crucial factor influencing regeneration dynamics. Our results support previous findings that bird-dispersed species are disproportionately affected by seed limitation (Gallegos et al., 2016; Saavedra et al., 2015). This suggests that restoration efforts should focus on increasing animal-mediated seed dispersal, either by planting animal-dispersed species accompanied by seed addition under intact bracken cover or by installing perches to attract seed dispersers (Mayta et al., 2024). These strategies could be combined and arranged in small islands, following applied nucleation, to enhance the recruitment of large-seeded late-successional species (Holl et al., 2020; Schubert et al., 2024; Zahawi et al., 2013).

The two restoration techniques tested here may be particularly relevant in bracken-dominated landscapes where forest regeneration is arrested (Christmann et al., 2023) and there is low seed arrival and poor seedling establishment. Our results support the notion that maintaining bracken cover could provide a protective microenvironment that mitigates extreme temperatures and improves soil moisture conditions, thereby promoting tree recruitment. Since bracken is shade-intolerant in the tropics (Xavier et al., 2019), bracken biomass will decrease once these species have overgrown bracken, and forest succession will proceed.

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Chapter VII. Synthesis

Synthesis

The aim of this thesis was to evaluate the role of bracken fronds and litter in early seedling development and to examine the functional traits that help to overcome the environmental filters in bracken-dominated areas. I tested whether the main components of bracken, i.e., fronds and litter, have facilitative or inhibitory effects on natural seedling recruitment, soil seed bank, and post-planting seedling establishment, recruitment, and growth in different experimental treatments involving their separate and combined removal. Additionally, I explored which plant functional traits enable species to overcome environmental filters in fire-disturbed habitats and I compared seedling performance by different sowing restoration techniques to identify the best combination of sowing technique and bracken management strategy. My results reveal the complex interplay between environmental conditions created by bracken, species traits and the effectiveness of restoration techniques to promote forest regeneration.

In chapter II, I evaluated the effect of bracken fronds and litter on natural seedling recruitment. I found a higher density and species diversity of naturally recruited seedlings in the treatment with bracken fronds and litter, particularly of animal-dispersed tree species, compared to those treatments where bracken fronds and litter were removed. I found a similar pattern for early-, mid- and late-successional tree species. Besides, I found that environmental conditions created by bracken, including light availability, soil temperature, and litter depth, influenced seedling density and species diversity, benefiting tree species while limiting the establishment of other life forms. These findings suggest that while bracken can hinder the recruitment of some species, it can also facilitate the regeneration of others. These results highlight the importance of a trait-based approach for selecting species to enhance restoration efforts in bracken-dominated habitats.

In chapter III, I evaluated the effect of bracken fronds and litter on the abundance, richness and diversity of the soil seed bank (SSB) in tropical montane fire-deforested areas. I found that species richness and diversity of tree and zoochorous species were highest in the presence of both fronds and litter and lowest in their absence. Species abundance was not affected by the removal of bracken fronds and litter. These results suggest that bracken fronds and litter create favorable microclimatic conditions that help to maintain species viability in the SSB, despite the limited seed arrival, and that they do not prevent seeds to be incorporated in the SSB.

In chapter IV, I investigated the facilitative and competitive roles of bracken fronds and litter on seedling establishment, recruitment success, and growth after 36 months, with a focus on seed size. Large-seeded species exhibited significantly higher establishment and recruitment success in the presence of both fronds and litter, whereas small-seeded species were negatively affected by litter accumulation. Fronds had an overall positive effect on all seed sizes, while litter primarily hindered seedling establishment of small-seeded species. Our results indicate that bracken fronds facilitate forest regeneration, while bracken litter imposes a significant barrier to small-seeded species during the early life stage, suggesting that seedling establishment is an important bottleneck for small-seeded species in bracken-dominated areas with accumulated litter. These findings highlight the importance of deepening our knowledge of plant-plant interactions in order to identify the main constraints to their environment and develop restoration strategies.

In chapter V, I analyzed which functional traits were related to a higher performance in bracken presence to guide species selection for active restoration in bracken-dominated areas. I identified eight functional traits that improved seedling performance under bracken, with a strong advantage for bird-dispersed, large-seeded species. Despite their ability to overcome bracken-related environmental filters, these species were not the most abundant in old-growth forests. My findings suggest that species with conservative traits are better suited to establish in bracken-dominated areas and that restoration efforts should conduct trait-based seed addition experiments to guide the species selection to enhance their ability to persist in these and other challenging conditions.

In chapter VI, I compared effectiveness of two restoration techniques, seed addition and seedling planting, on seedling performance of tree species under different bracken management treatments. The complete removal of fronds and litter led to lower seedling recruitment for both restoration techniques, suggesting that intact bracken provides a protective microenvironment for seedlings. Our results indicate that combining seed addition and seedling planting, with a focus on stress-tolerant, animal-dispersed species with advantageous functional traits, could enhance restoration success in bracken-dominated environments.

Discussion

Given the increase in fires in the tropical region (Aguilar-Garavito & Cortina, 2023; Oliveras et al., 2018), the control of bracken remains a major challenge in tropical forest restoration (Levy-Tacher & Morón-Ríos, 2023). The results that I present in all chapters showed that bracken fronds and litter influence species recruitment. However, based on a trait-based approach I was capable to elucidate which species can overcome these filters. In Chapter II, I show experimental evidence about a relationship of micro-environmental conditions created by bracken and natural seedling recruitment. Although tree density and species diversity were lower in bracken-dominated areas compared to the forest interior, they were significantly higher in treatments where both fronds and litter were present. In contrast, treatments without fronds and litter exhibited the lowest tree seedling density and species diversity. This pattern was consistent for both wind- and animal-dispersed species as well as for early- mid- and late-successional species, probably due to the low humidity and higher temperatures in open areas causing seedling mortality due to desiccation (Alvarez-Aquino et al., 2004; Khurana & Singh, 2001). Plant species vary in their light requirements to germinate, establish and grow (Montgomery & Chazdon, 2002). My study reveals that lower levels of photosynthetically active radiation were associated with higher tree density and species diversity, suggesting that tree species tolerate shade under a bracken canopy and their recruitment could be improved by bracken fronds. Previous research in bracken-dominated areas showed similar results, indicating that bracken has a differential effect which benefits late-successional species but may hinder the establishment of pioneer species (Günter et al., 2007; Ssali et al., 2019). In Chapter III, I found a similar pattern, with the persistence and emergence of the soil seed bank favored by the presence of bracken fronds and litter. The short viability of most large animal-dispersed seeds in the tropics implies that many of these species are also absent from the soil seed bank (Lippok et al., 2013). Although in natural recruitment and SSB, few of the seedlings recorded in the bracken-dominated areas corresponded to animal-dispersed and late-successional species, I found evidence that bracken promotes their recruitment, and that their low density is likely related to dispersal limitation, as previously reported in the study area (Gallegos et al., 2016; Saavedra et al., 2015).

In Chapter IV, I further explored these contrasting effects, and found support that bracken fronds facilitated seedling establishment, recruitment, and growth. In contrast, bracken litter acted as a barrier for seedling establishment of small-seeded species. However, the seed addition experiment showed that although small-seeded species had significantly lower establishment and recruitment than medium- and large-seeded species, their performance were also improved in treatments where fronds and litter were present. This suggests that the microclimatic buffering provided by bracken fronds can mitigate some of the environmental stressors in open areas, such as high temperatures and low soil moisture, which are known to limit seedling survival (Gallegos et al., 2015). These results corroborate that medium- and large-seeded species are better adapted to shaded conditions (Wang et al., 2022), which are typical of bracken-dominated areas, since the light requirements for germination and establishment decrease with increasing seed size (Milberg et al., 2000). The presence of bracken litter also acted as a physical barrier, hindering small-seeded species, likely due to their lower energy reserves, which limit their ability to emerge through thick litter layers (Jessen et al., 2023; Moles & Westoby, 2004).

While seed size played a key role in determining recruitment success, our results suggest that it does not fully explain the variability observed among species. For instance, some small-seeded and animal-dispersed species, such as *Miconia hygrophila*, performed better than others, indicating that additional functional traits than seed size may also influence seedling survival under bracken.

In Chapter V, I further assessed the role of functional traits in shaping species responses to bracken presence. Traits related to conservative strategies such as large seed size, thick bark, high stem-specific density (SSD), and low specific leaf area (SLA) enhanced seed germination in bracken presence. Conversely, traits associated with acquisitive strategies, such as low leaf dry matter content (LDMC) and high leaf area (LA), enhanced relative growth rate (RGR). These findings align with previous chapters, reinforcing that species with stress-tolerant traits are better suited for establishing in bracken-dominated landscapes. My results highlight that seed size play a central role in seedling establishment, with larger seeds leading to higher germination and survival rates, likely due to their greater energy reserves, which enhance seedling emergence and early survival under stressful conditions (Baraloto et al., 2005; Baraloto & Forget, 2007; Milberg et al., 2000). However, this advantage comes at the cost of lower relative growth rates, reflecting a well-documented growth-survival trade-off (Rüger et al., 2018). Beyond seed size, my findings suggest that other functional traits are also critical for overcoming the environmental filters imposed by bracken. Species with short adult stature had higher recruitment success, likely because they commonly have high recruitment rates, reproduce at a smaller size, have shorter generation times, and exhibit greater drought resistance (Fajardo et al., 2019; Rüger et al., 2018). These traits can be advantageous for species in bracken-dominated areas, where frequent fires and competition for light create selective pressures favoring species with conservative life-history strategies, such as high stem-specific density, thick bark, and low specific leaf area (Vile et al., 2005). My results also highlight the importance of bird-dispersed species in natural recruitment, as most species that successfully established in my experiment were dispersed by birds. Given the strong dispersal limitation in these degraded landscapes, my results suggest that restoration strategies should prioritize the introduction of species with high establishment probabilities, particularly short-statured, bird-dispersed trees with large seeds.

A key challenge in restoring bracken-dominated areas is determining the most effective intervention. My results in Chapter VI showed that seedling planting significantly outperformed seed addition in terms of recruitment success and growth across all bracken treatments. This aligns with previous studies that have found seedling planting to be a more reliable technique in degraded environments with strong environmental filters, as nursery-raised seedlings benefit from greater biomass accumulation and resource storage before field transplantation (Holl et al., 2011; Zahawi & Holl, 2014). However, seed addition showed a high potential for species with traits favoring early establishment, particularly when seeds were sown without litter accumulation, supporting the idea that direct seeding can be effective under certain microsite conditions (Bonilla-Moheno & Holl, 2010; Cole et al., 2011; Douterlungne et al., 2010). These findings reinforce the patterns observed in previous studies and chapters, where strong dispersal limitation were identified as a key barrier to recruitment in fire-disturbed landscapes (Gallegos et al., 2016).

The complete removal of bracken fronds and litter resulted in lower recruitment for both restoration techniques. This aligns with my findings on natural seedling recruitment (Chapter II), suggesting that bracken, rather than being detrimental, can provide crucial shelter against harsh post-fire conditions, particularly for species with large seeds and shade tolerance (Cole et al., 2011; Ssali et al., 2019; Toledo-Aceves et al., 2022). Additionally, these results support previous findings that bracken, as well as other ferns, may indirectly benefit seedlings by reducing competition with grasses and providing some protection from herbivores (Azevedo-Schmidt et al., 2024). These results contribute to the broader discussion of restoration strategies (Chapters II and IV), highlighting that an integrated approach is needed. While seedling planting ensures higher initial survival, selective seed addition can complement it by targeting species with traits suited for early establishment, with the possibility to be introduced in broader areas. Although mechanical control and tree planting of pioneer species have been suggested as effective strategies for promoting forest recovery in bracken-dominated areas (Douterlungne et al., 2013; Levy-Tacher et al., 2015; Xavier et al., 2019, 2023), my results highlight the complexity of the role of bracken in regeneration dynamics. Rather than complete bracken removal, restoration efforts should consider selecting species with traits that benefit from bracken presence, reducing or eliminating the need for intensive control. I observed that relative growth rates were also lower in treatments where fronds and litter were removed, suggesting that early seedling development depends more on microclimatic stability (Chapter II). A more realistic and cost-effective approach would be to integrate seed addition and seedling planting of animal-dispersed species to enhance seed disperser activity and increase seed rain in bracken-dominated areas (De La Peña-Domene et al., 2014).

The findings of this thesis contribute to the development of more effective restoration strategies for fire-disturbed tropical montane forests. Given the dual limitations of dispersal and establishment in fire-disturbed landscapes, restoration strategies should integrate seed dispersal enhancement, attracting frugivorous dispersers to increase seed rain, such as bird perches, as showed in a parallel study (Mayta et al., 2024). This thesis underscores the importance of integrating ecological knowledge into restoration planning. Understanding how species traits interact with environmental constraints allows for interventions that align with natural successional processes, to foster forest recovery. Future research should prioritize long-term monitoring of recruitment dynamics, to assess how different restoration strategies influence ecosystem resilience and recovery over time. Evaluating species performance across successional stages will be key to refining restoration practices in bracken-dominated landscapes.

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Appendices

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Supplementary material Chapter II

Table S1. Species list of naturally recruiting seedlings in bracken-dominated areas and the forest, including family, the number of individuals recorded, dispersal vector, successional status, woodiness and life form; W: Wind-dispersed species, A: Animal-dispersed species, E: Early-successional species, M: Mid-successional species, L: Late-successional species. Undetermined species present a voucher code. All specimens are stored at the Herbario Nacional de Bolivia (LPB).

Family	Species	Number of individuals	Dispersal vector	Successional stage	Woodiness	Life form
Acanthaceae	*Acanthaceae* sp. CLA 864	3	W	L	Non-woody	Shurb
Acanthaceae	*Acanthaceae* sp. CLA 924	1	W	L	Non-woody	Shurb
Acanthaceae	*Justicia* sp. CLA 1006	12	W	L	Non-woody	Shurb
Acanthaceae	*Ruellia* sp. CLA 923	1	W	L	Non-woody	Shurb
Amaranthaceae	*Alternanthera flavescens*	3	W	E	Non-woody	Herb
Anacardiaceae	*Mauria heterophylla*	4	A	M	Woody	Tree
Annonaceae	*Guatteria glauca*	2	A	L	Woody	Tree
Apiaceae	*Eryngium elegans*	32	W	E	Non-woody	Herb
Apiaceae	*Eryngium rauhianum*	2	W	E	Non-woody	Herb
Apocynaceae	*Macropharynx gigantea*	1	W	L	Woody	Shurb
Apocynaceae	*Mandevilla brachyloba*	2	W	E	Woody	Vine
Aquifoliaceae	*Ilex goudotii*	2	A	L	Woody	Tree
Araceae	*Anthurium scandens*	3	A	L	Non-woody	Vine
Araceae	*Anthurium weberbaueri*	2	A	L	Non-woody	Vine
Araceae	*Philodendron ornatum*	16	A	L	Non-woody	Herb
Araliaceae	*Oreopanax membranaceus*	2	A	L	Woody	Tree
Araliaceae	*Oreopanax* sp. CLA 533	2	A	L	Woody	Tree
Arecaceae	*Arecaceae* sp. CLA 868	2	A	L	Woody	Tree
Arecaceae	*Geonoma* sp. CLA 915	12	A	L	Woody	Tree
Asclepiadaceae	*Blepharodon salicinum*	15	W	E	Woody	Vine
Asteraceae	*Achyrocline ramosissima*	6	W	E	Non-woody	Shurb
Asteraceae	*Asteraceae* sp. CLA 476	1	W	E	Non-woody	Shurb
Asteraceae	*Asteraceae sp.* CLA 485	4	W	E	Non-woody	Shurb
Asteraceae	*Asteraceae* sp. CLA 514	2	W	E	Non-woody	Shurb
Asteraceae	*Asteraceae* sp. CLA 519	1	W	E	Non-woody	Shurb
Asteraceae	*Asteraceae* sp. CLA 536	2	W	E	Non-woody	Shurb
Asteraceae	*Austroeupatorium decemflorum*	2	W	E	Woody	Shurb
Asteraceae	*Austroeupatorium inulifolium*	12	W	E	Woody	Shurb
Asteraceae	*Baccharis dracunculifolia*	4	W	E	Woody	Shurb
Asteraceae	*Baccharis genistelloides*	78	W	E	Woody	Shurb
Asteraceae	*Baccharis latifolia*	7	W	E	Woody	Shurb
Asteraceae	*Baccharis linearifolia*	26	W	E	Woody	Shurb
Asteraceae	*Baccharis linearifolia* subsp. *chilco*	9	W	E	Woody	Shurb

Asteraceae	*Baccharis nitida*	187	W	E	Woody	Shurb
Asteraceae	*Baccharis oblongifolia*	1	W	M	Woody	Shurb
Asteraceae	*Baccharis platypoda*	7	W	E	Woody	Shurb
Asteraceae	*Baccharis* sp. CLA 844	1	W	E	Woody	Shurb
Asteraceae	*Baccharis trinervis* var. *debilis*	7	W	E	Woody	Shurb
Asteraceae	*Calea solidaginea*	1	W	E	Woody	Shurb
Asteraceae	*Chevreulia acuminata*	8	W	E	Non-woody	Herb
Asteraceae	*Critoniopsis yungasensis*	6	W	L	Woody	Shurb
Asteraceae	*Dendrophorbium biacuminatum*	7	W	E	Woody	Shurb
Asteraceae	*Dendrophorbium curvidens*	9	W	E	Woody	Shurb
Asteraceae	*Dendrophorbium multinerve*	1	W	E	Woody	Shurb
Asteraceae	*Jungia pauciflora*	3	W	L	Non-woody	Herb
Asteraceae	*Kaunia gynoxymorpha*	1	W	E	Woody	Shurb
Asteraceae	*Kaunia* sp. CLA 867	2	W	E	Woody	Shurb
Asteraceae	*Lepidaploa canescens*	1	W	L	Woody	Shurb
Asteraceae	*Lepidaploa sordidopapposa*	3	W	L	Woody	Shurb
Asteraceae	*Mikania baccharoidea*	2	W	L	Woody	Shurb
Asteraceae	*Mikania banisteriae*	2	W	L	Woody	Shurb
Asteraceae	*Mikania comarapensis*	3	W	L	Woody	Shurb
Asteraceae	*Mikania longiacuminata*	16	W	L	Woody	Shurb
Asteraceae	*Mikania officinalis*	12	W	E	Non-woody	Shurb
Asteraceae	*Mikania* sp. CLA 1013	1	W	L	Woody	Shurb
Asteraceae	*Mikania* sp. CLA 118	1	W	L	Woody	Shurb
Asteraceae	*Moquiniastrum bolivianum*	1	W	E	Non-woody	Shurb
Asteraceae	*Munnozia gigantea*	4	W	E	Non-woody	Shurb
Asteraceae	*Munnozia glandulosa*	26	W	E	Non-woody	Shurb
Asteraceae	*Munnozia maronii*	17	W	E	Non-woody	Shurb
Asteraceae	*Ophryosporus kuntzei*	23	W	E	Woody	Shurb
Asteraceae	*Ophryosporus piquerioides*	6	W	E	Woody	Shurb
Asteraceae	*Oyedaea boliviana*	20	W	E	Woody	Shurb
Asteraceae	*Raulinoreitzia crenulata*	130	W	E	Woody	Shurb
Asteraceae	*Rubiaceae* sp. CLA 1025	1	W	L	Woody	Shurb
Asteraceae	*Stevia boliviensis*	10	W	E	Non-woody	Herb
Asteraceae	*Verbesina leucactinota*	1	W	E	Woody	Shurb
Asteraceae	*Verbesina* sp. CLA 515	9	W	E	Woody	Shurb
Asteraceae	*Vernonanthura patens*	1	W	L	Woody	Tree
Blechnaceae	*Blechnum fragile*	13	W	L	Non-woody	Herb
Blechnaceae	*Blechnum malacothrix*	16	W	E	Non-woody	Herb
Blechnaceae	*Blechnum malacothrix*	33	W	E	Non-woody	Herb
Boraginaceae	*Varronia cylindristachia*	1	A	E	Woody	Tree
Bromeliaceae	*Racinaea parviflora*	3	W	L	Non-woody	Herb
Campanulaceae	*Siphocampylus corymbifer*	1	W	E	Woody	Shurb
Campanulaceae	*Siphocampylus rusbyanus*	4	W	E	Woody	Shurb

Caprifoliaceae	*Valeriana clematitis*	2	W	E	Non-woody	Vine
Caryophyllaceae	*Arenaria lanuginosa*	12	W	E	Woody	Shurb
Caryophyllaceae	*Paronychia setigera*	18	W	E	Non-woody	Herb
Chloranthaceae	*Hedyosmum angustifolium*	7	A	L	Woody	Tree
Chloranthaceae	*Hedyosmum racemosum*	6	A	M	Woody	Tree
Clethraceae	*Clethra cuneata*	1	W	L	Woody	Tree
Clethraceae	*Clethra revoluta*	19	W	L	Woody	Tree
Clethraceae	*Clethra scabra*	100	W	M	Woody	Tree
Clusiaceae	*Clusia elongata*	20	A	L	Woody	Tree
Clusiaceae	*Clusia lechleri*	7	A	L	Woody	Tree
Clusiaceae	*Clusia trochiformis*	2	A	M	Woody	Tree
Costaceae	*Costus* sp. CLA 988	1	A	L	Non-woody	Herb
Cucurbitaceae	*Cucurbitaceae* sp. CLA 520	2	A	E	Non-woody	Herb
Cunoniaceae	*Weinmannia sorbifolia*	72	W	E	Woody	Tree
Cyclanthaceae	*Cyclanthaceae* sp. CLA 678	1	A	E	Non-woody	Herb
Dioscoreaceae	*Dioscorea* sp. CLA 477	2	W	M	Non-woody	Vine
Dioscoreaceae	*Dioscorea* sp. CLA 531	1	W	M	Non-woody	Vine
Dioscoreaceae	*Dioscorea* sp. CLA 825	17	W	M	Non-woody	Vine
Dioscoreaceae	*Dioscorea* sp. SA	1	W	M	Non-woody	Vine
Dryopteridaceae	*Elaphoglossum* sp CLA 807	1	W	L	Non-woody	Herb
Dryopteridaceae	*Elaphoglossum* sp. CLA 1027	9	W	L	Non-woody	Herb
Ericaceae	*Bejaria aestuans*	57	W	M	Woody	Tree
Ericaceae	*Cavendishia pubescens*	5	A	M	Woody	Shurb
Ericaceae	*Gaultheria buxifolia* var. *secunda*	2	A	E	Woody	Shurb
Ericaceae	*Gaultheria erecta*	125	A	E	Woody	Shurb
Ericaceae	*Gaultheria eriophylla*	22	A	E	Woody	Shurb
Ericaceae	*Gaultheria eriophylla* var. *mucronata*	1	A	E	Woody	Shurb
Ericaceae	*Vaccinium floribundum*	1	A	E	Woody	Shurb
Euphorbiaceae	*Acalypha* sp. SGA 5404	1	A	L	Woody	Shurb
Euphorbiaceae	*Alchornea brittonii*	1	A	L	Woody	Tree
Euphorbiaceae	*Alchornea glandulosa*	1	A	L	Woody	Tree
Euphorbiaceae	*Alchornea triplinervia* var. *montana*	3	A	M	Woody	Tree
Euphorbiaceae	*Tragia* sp. SGA 4035	2	W	E	Non-woody	Vine
Fabaceae	*Chamaecrista glandulosa*	46	W	E	Non-woody	Shurb
Fabaceae	*Collaea speciosa*	133	W	E	Woody	Shurb
Fabaceae	*Cologania broussonetii*	1	W	E	Non-woody	Herb
Fabaceae	*Crotalaria micans*	6	W	E	Non-woody	Shurb
Fabaceae	*Crotalaria nitens*	49	W	E	Non-woody	Shurb
Fabaceae	*Desmodium barbatum*	1	W	E	Non-woody	Shurb
Fabaceae	*Desmodium incanum*	10	W	E	Non-woody	Shurb
Fabaceae	*Desmodium limense*	4	W	E	Non-woody	Shurb
Fabaceae	*Desmodium subsericeum*	6	W	E	Non-woody	Shurb
Fabaceae	*Desmodium yungasense*	4	W	E	Non-woody	Shurb

Fabaceae	*Fabaceae* sp. SA	5	W	E	Non-woody	Shurb
Fabaceae	*Inga adenophylla*	2	A	E	Woody	Tree
Fabaceae	*Inga fendleriana*	2	A	L	Woody	Tree
Fabaceae	*Inga sapindoides*	3	A	L	Woody	Tree
Fabaceae	*Macroptilium* sp. CLA 585	1	W	E	Non-woody	Herb
Fabaceae	*Mimosa boliviana*	2	W	E	Woody	Shurb
Fabaceae	*Rhynchosia edulis*	1	W	E	Non-woody	Shurb
Gentianaceae	*Chelonanthus acutangulus*	1	W	E	Woody	Herb
Gentianaceae	*Macrocarpaea bangiana*	149	W	E	Woody	Shurb
Gentianaceae	*Symbolanthus australis*	1	W	L	Woody	Shurb
Gentianaceae	*Tapeinostemon* sp. CLA 757	1	W	L	Non-woody	Herb
Gleicheniaceae	*Sticherus* sp. CLA 1002	4	W	E	Non-woody	Herb
Hypericaceae	*Vismia crassa*	5	A	E	Woody	Tree
Hypericaceae	*Vismia glaziovii*	2	A	L	Woody	Tree
Hypericaceae	*Vismia rusbyi*	3	A	L	Woody	Tree
Lamiaceae	*Hyptidendron arboreum*	5	W	L	Woody	Tree
Lamiaceae	*Hyptis mutabilis*	15	W	E	Non-woody	Shurb
Lamiaceae	*Hyptis odorata*	8	W	E	Woody	Shurb
Lamiaceae	*Hyptis uncinata*	1	W	E	Non-woody	Shurb
Lamiaceae	*Lepechinia* sp. CLA 829	6	W	E	Woody	Shurb
Lauraceae	*Aiouea montana*	4	A	M	Woody	Tree
Lauraceae	*Aniba* sp. CMR 438	2	A	L	Woody	Tree
Lauraceae	*Beilschmiedia latifolia*	3	A	L	Woody	Tree
Lauraceae	*Beilschmiedia tovarensis*	1	A	L	Woody	Tree
Lauraceae	*Nectandra acutifolia*	19	A	L	Woody	Tree
Lauraceae	*Nectandra cuspidata*	27	A	L	Woody	Tree
Lauraceae	*Ocotea puberula*	1	A	M	Woody	Tree
Lauraceae	*Persea subcordata*	1	A	L	Woody	Tree
Lythraceae	*Cuphea weddelliana*	16	W	E	Non-woody	Herb
Malpighiaceae	*Malpighiaceae* sp. CLA 488	2	W	E	Woody	Tree
Malpighiaceae	*Malpighiaceae* sp. CLA 957	1	W	E	Woody	Tree
Melastomataceae	*Desmoscelis calcarata*	37	W	E	Non-woody	Shurb
Melastomataceae	*Leandra carassana*	4	A	E	Woody	Shurb
Melastomataceae	*Meriania axinioides*	1	W	L	Woody	Tree
Melastomataceae	*Meriania boliviensis*	1	W	L	Woody	Tree
Melastomataceae	*Meriania brittoniana*	3	W	L	Woody	Tree
Melastomataceae	*Miconia cordata*	5	A	E	Woody	Shurb
Melastomataceae	*Miconia cyanocarpa* var. *dendritica*	15	A	E	Woody	Shurb
Melastomataceae	*Miconia cyanocarpa* var. *hirsuta*	17	A	E	Woody	Shurb
Melastomataceae	*Miconia cyanocarpa* var. *parvifolia*	17	A	E	Woody	Shurb
Melastomataceae	*Miconia hygrophila*	25	A	E	Woody	Tree
Melastomataceae	*Miconia leacrenata*	204	A	E	Woody	Shurb
Melastomataceae	*Miconia leacrenata* var. *rotundifolia*	31	A	E	Woody	Shurb

Melastomataceae	*Miconia micropetala*	3	A	E	Woody	Tree
Melastomataceae	*Miconia plumifera*	2	A	E	Woody	Shurb
Melastomataceae	*Miconia rugosa grupo leandra*	19	A	E	Woody	Shurb
Melastomataceae	*Miconia staphidioides*	1	A	E	Woody	Shurb
Melastomataceae	*Miconia theaezans*	3	A	E	Woody	Tree
Melastomataceae	*Miconia uvifera*	3	A	E	Woody	Shurb
Melastomataceae	*Miconia* vel sp. nov SGA 3863	6	A	E	Woody	Shurb
Melastomataceae	*Miconia* vel sp. nov SGA 5056	2	A	E	Woody	Shurb
Melastomataceae	*Tibouchina brittoniana*	418	W	E	Woody	Shurb
Melastomataceae	*Tibouchina confertiflora*	1	W	E	Woody	Shurb
Melastomataceae	*Tibouchina longifolia*	23	W	E	Woody	Shurb
Melastomataceae	*Tibouchina stenocarpa* var. *boliviensis*	18	W	E	Woody	Shurb
Meliaceae	*Cedrela odorata*	1	W	L	Woody	Tree
Meliaceae	*Trichilia sp.* CLA 539	5	A	L	Woody	Tree
Monimiaceae	*Mollinedia lanceolate*	4	A	L	Woody	Tree
Monimiaceae	*Mollinedia repanda*	2	A	L	Woody	Tree
Monimiaceae	*Mollinedia steinbachiana*	3	A	L	Woody	Tree
Myricaceae	*Morella pubescens*	13	A	M	Woody	Tree
Myrtaceae	*Myrcia* cf. *fallax*	1	A	L	Woody	Tree
Myrtaceae	*Myrcia fallax*	15	A	L	Woody	Tree
Myrtaceae	*Myrcia lonchophylla*	2	A	L	Woody	Tree
Myrtaceae	*Myrcia paivae*	17	A	E	Woody	Tree
Myrtaceae	*Myrcia splendens*	5	A	M	Woody	Tree
Myrtaceae	*Myrcia subglabra*	1	A	L	Woody	Tree
Orchidaceae	*Psilochilus modestus*	2	A	L	Non-woody	Herb
Passifloraceae	*Passiflora dalechampioides*	1	A	L	Woody	Shurb
Phyllanthaceae	*Hieronyma fendleri*	2	A	M	Woody	Tree
Phyllanthaceae	*Phyllanthus* sp. CLA 577	2	A	L	Non-woody	Shurb
Piperaceae	*Peperomia trinervis*	14	A	L	Non-woody	Herb
Piperaceae	*Piper bolivianum*	4	A	L	Woody	Tree
Piperaceae	*Piper elongatum*	10	A	E	Woody	Tree
Piperaceae	*Piper puberulinerve*	4	A	L	Woody	Shurb
Piperaceae	*Piper pubiovarium*	1	A	L	Woody	Shurb
Piperaceae	*Piper trichorhachis*	6	A	L	Woody	Shurb
Piperaceae	*Piper trigoniastrifolium*	2	A	L	Woody	Shurb
Poaceae	*Chusquea* sp. CLA 1062	7	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 1107	1	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 493	7	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 570	13	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 752	3	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 769	5	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 846	1	W	L	Woody	Vine
Poaceae	*Chusquea* sp. CLA 871	1	W	L	Woody	Vine

Poaceae	*Panicum* sp. CLA 534	11	W	E	Non-woody	Herb
Poaceae	*Poaceae* sp. CLA 1028	3	W	E	Non-woody	Herb
Poaceae	*Poaceae* sp. CLA 641	10	W	E	Non-woody	Herb
Polygalaceae	*Monnina* sp. CLA 641	38	W	E	Woody	Shurb
Polygalaceae	*Polygalaceae* sp. CLA 734	1	W	E	Non-woody	Herb
Polypodiaceae	*Niphidium albopunctatissimum*	2	W	L	Non-woody	Herb
Polypodiaceae	*Polypodiaceae* sp. CLA 483	1	W	L	Non-woody	Shurb
Polypodiaceae	*Serpocaulon levigatum*	25	W	L	Non-woody	Herb
Primulaceae	*Geissanthus bangii*	1	A	L	Woody	Tree
Primulaceae	*Myrsine coriacea*	79	A	M	Woody	Tree
Primulaceae	*Myrsine latifolia*	2	A	L	Woody	Tree
Primulaceae	*Myrsine pellucida*	10	A	L	Woody	Tree
Proteaceae	*Panopsis pearcei*	3	A	E	Woody	Tree
Proteaceae	*Roupala montana*	18	W	E	Woody	Tree
Pteridaceae	*Lophosoria quadripinnata*	1	W	E	Non-woody	Herb
Pteridaceae	*Pteridaceae* sp. 1	2	W	L	Non-woody	Herb
Pteridaceae	*Pteridaceae* sp. 2	3	W	L	Non-woody	Herb
Pteridaceae	*Pteris deflexa*	5	W	L	Non-woody	Herb
Rhamnaceae	*Rhamnus sphaerosperma*	9	A	M	Woody	Tree
Rosaceae	*Rubus adenothallus*	18	A	E	Woody	Shurb
Rosaceae	*Rubus boliviensis*	13	A	E	Woody	Shurb
Rubiaceae	*Borreria capitata*	33	W	E	Non-woody	Herb
Rubiaceae	*Borreria pazensis*	75	W	E	Non-woody	Herb
Rubiaceae	*Coccocypselum lanceolatum*	51	A	E	Non-woody	Herb
Rubiaceae	*Faramea* sp. CLA 653	2	A	L	Woody	Tree
Rubiaceae	*Galium hypocarpium*	24	A	E	Non-woody	Herb
Rubiaceae	*Galium noxium*	45	A	E	Non-woody	Herb
Rubiaceae	*Manettia hispida*	2	W	L	Woody	Tree
Rubiaceae	*Notopleura epiphytica*	1	A	L	Woody	Shurb
Rubiaceae	*Notopleura* sp. CLA 546	5	A	L	Woody	Shurb
Rubiaceae	*Palicourea attenuata*	7	A	L	Woody	Shurb
Rubiaceae	*Palicourea bryophila*	1	A	L	Woody	Shurb
Rubiaceae	*Palicourea buchtienii*	50	A	L	Woody	Shurb
Rubiaceae	*Palicourea flaviflora*	1	A	L	Woody	Tree
Rubiaceae	*Palicourea reticulata*	10	A	L	Woody	Tree
Rubiaceae	*Palicourea* sp. CLA 592	1	A	L	Woody	Shurb
Rubiaceae	*Palicourea tristis*	6	A	L	Woody	Tree
Rubiaceae	*Psychotria carthagenensis*	11	A	M	Woody	Shurb
Rubiaceae	*Randia* vel sp nov.	2	A	L	Woody	Shurb
Rubiaceae	*Rubiaceae* sp. CLA 967	2	A	L	Woody	Shurb
Sapindaceae	*Dodonaea viscosa*	1	W	E	Woody	Shurb
Sapindaceae	*Paullinia boliviana*	2	A	L	Woody	Tree
Sapindaceae	*Serjania dumicola*	2	W	L	Woody	Liana

Sapindaceae	*Serjania pannifolia*	3	W	L	Woody	Liana
Sapindaceae	*Serjania* sp. CLA 939	3	W	L	Woody	Liana
Siparunaceae	*Siparuna aspera*	6	A	L	Woody	Tree
Siparunaceae	*Siparuna grandiflora*	9	A	L	Woody	Tree
Siparunaceae	*Siparuna tomentosa*	3	A	L	Woody	Tree
Smilacaceae	*Smilax cognata*	2	A	E	Woody	Vine
Smilacaceae	*Smilax quinquenervia*	1	A	E	Woody	Vine
Smilacaceae	*Smilax tomentosa*	2	A	E	Woody	Vine
Solanaceae	*Solanum clandestinum*	1	A	L	Woody	Shurb
Symplocaceae	*Symplocos arechea*	1	A	M	Woody	Tree
Symplocaceae	*Symplocos mapiriensis*	3	A	L	Woody	Tree
Thelypteridaceae	*Thelypteris* sp. CLA 541	4	W	L	Non-woody	Herb
Urticaceae	*Myriocarpa stipitata*	1	W	M	Woody	Shurb
Urticaceae	*Pilea cymbifolia*	3	A	L	Non-woody	Shurb
Urticaceae	*Cecropia elongata*	4	A	E	Woody	Tree
Verbenaceae	*Lantana* sp. CLA 913	3	A	E	Non-woody	Shurb
Viburnaceae	*Viburnum ayavacense*	7	A	E	Woody	Shurb
Viburnaceae	*Viburnum halii*	1	A	E	Woody	Shurb
Viburnaceae	*Viburnum incarum*	1	A	E	Woody	Shurb
Viburnaceae	*Viburnum seemenii*	7	A	E	Woody	Shurb
Violaceae	*Viola boliviana*	9	W	E	Non-woody	Herb

Table S2. Details on the abundance of seedlings according to their life-form (tree, shrub, herb, vine), dispersal vector, and successional status n bracken-dominated areas and in the forest interior.

	Life-form	**Bracken**	**Forest**
Trees	Total	460	241
	Animal-dispersed	184	231
	Wind-dispersed	276	10
	Early-successional	125	12
	Mid-successional	305	20
	Late-successional	29	209
Shrubs	Total	2102	213
	Animal-dispersed	497	136
	Wind-dispersed	1605	77
	Early-successional	2061	59
	Mid-successional	6	12
	Late-successional	35	142
Herbs	Total	383	132
	Animal-dispersed	117	39
	Wind-dispersed	266	93
	Early-successional	379	31
	Mid-successional	0	0
	Late-successional	4	101
Vines	Total	49	49
	Animal-dispersed	4	6
	Wind-dispersed	45	43
	Early-successional	22	4
	Mid-successional	20	1
	Late-successional	7	44

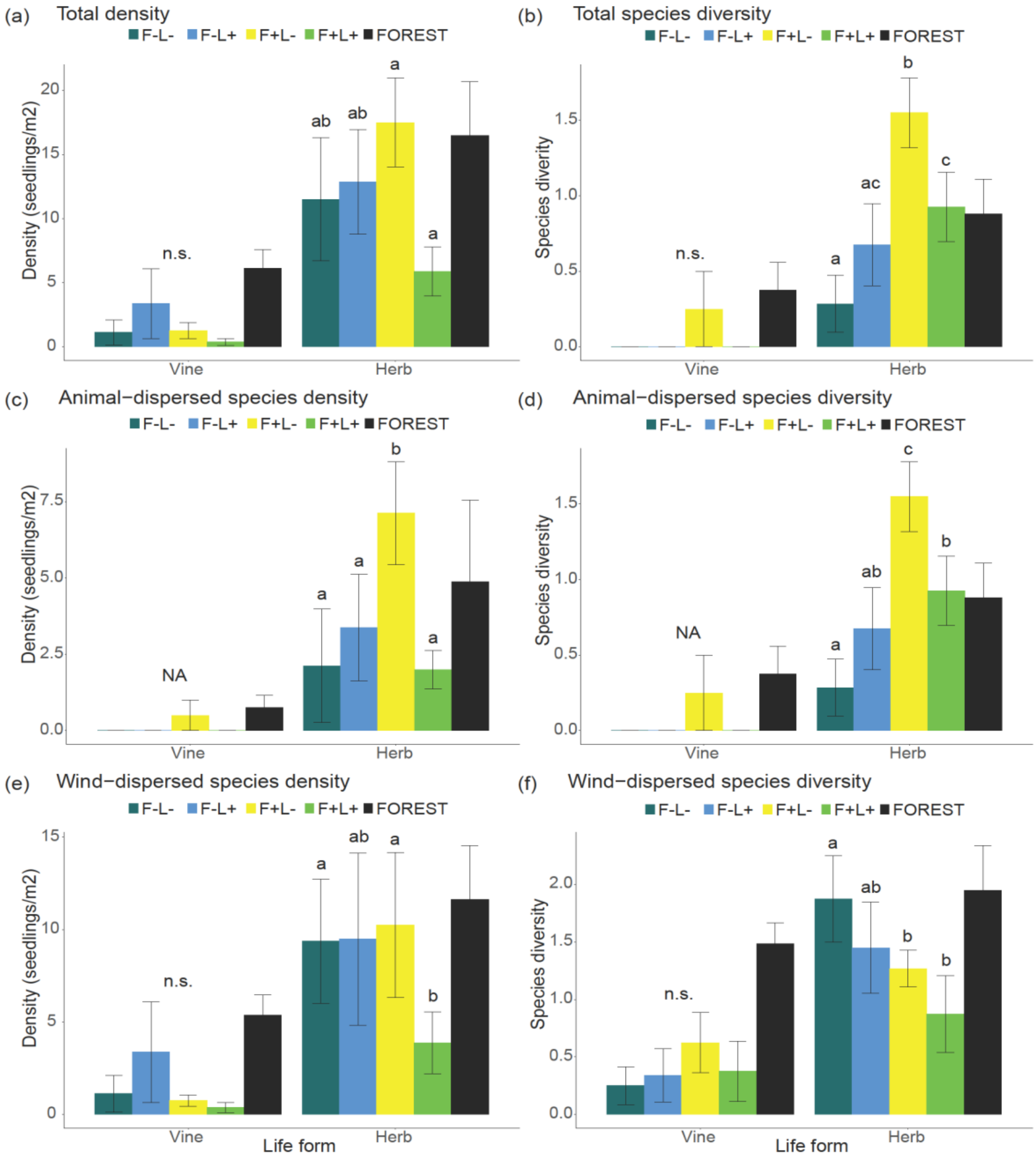


Fig. S1. Density (left panels) and species diversity (Hill number q1, right panels) of: (a-b) total, (c-d) animal-dispersed, and (e-f) wind-dispersed naturally recruiting seedlings under different bracken treatments: with fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Different letters denote significant differences among treatments ($p < 0.05$), n.s. indicates no significant differences ($p>0.05$). NA denotes no feasible comparison. Shown are means ± SE.

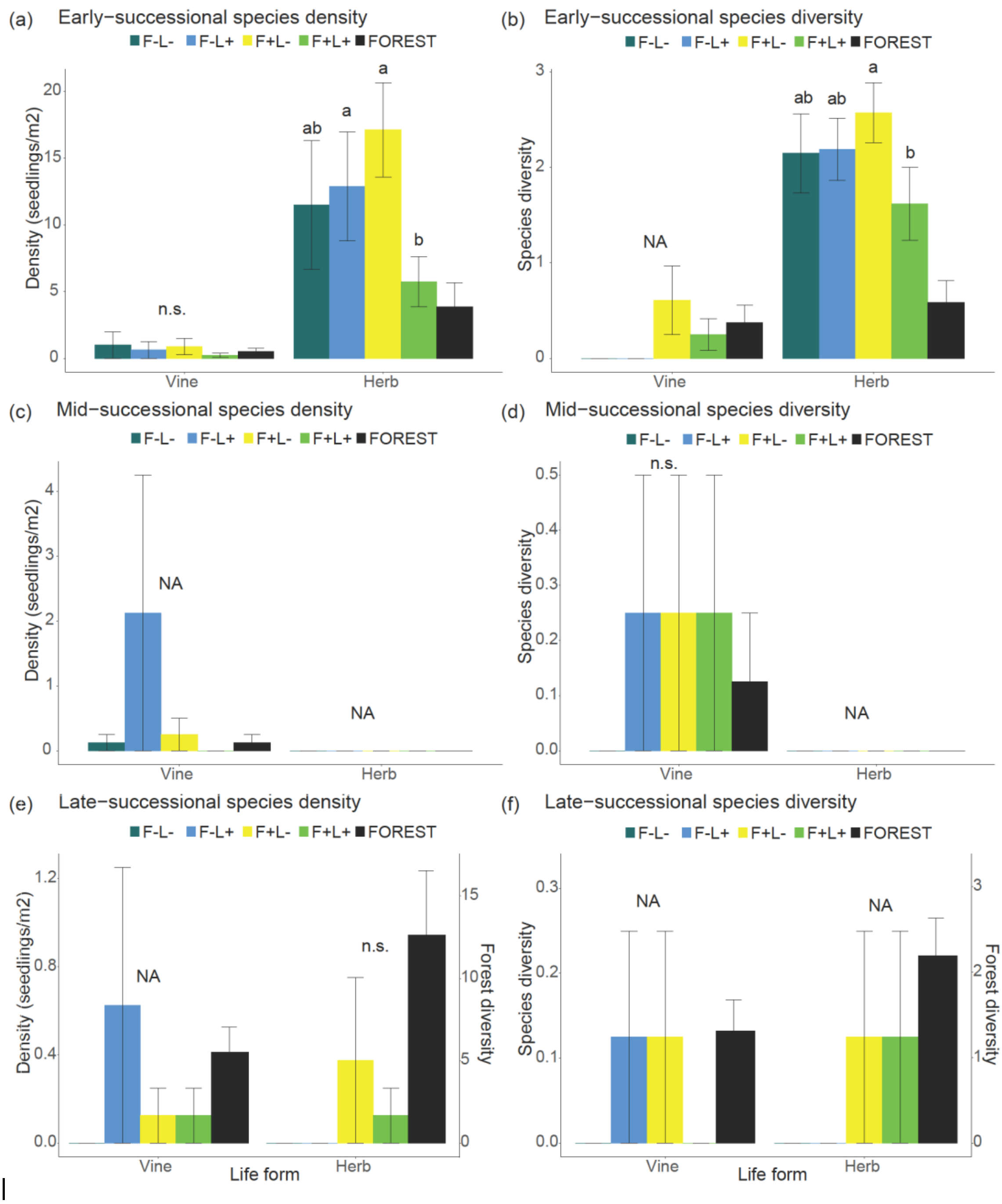


Fig. S2. Density (left panels) and species diversity (Hill number q1, right panels, right panels) of: early- (a-b), mid-(c-d), and late-successional (e-f) naturally recruiting seedlings under different bracken treatments: with fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Different letters denote significant differences among treatments ($p < 0.05$), n.s. indicates no significant differences ($p>0.05$). NA denotes no feasible comparison. Shown are means ± SE.

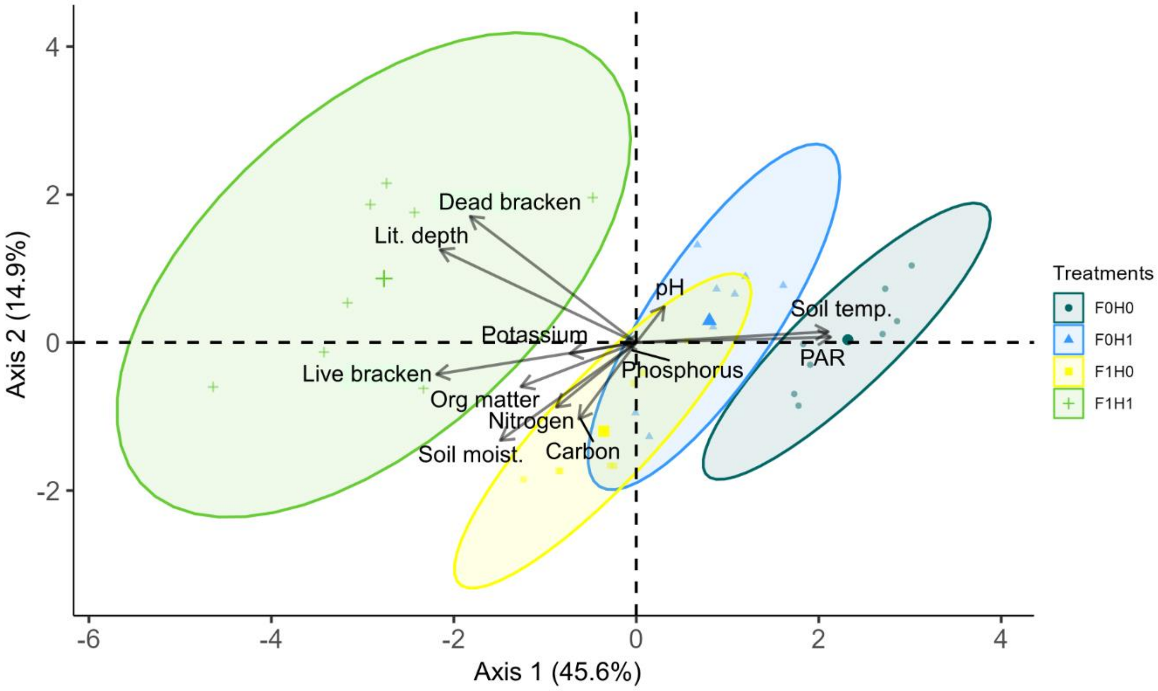


Fig. S3. Principal component analysis (PCA) of 12 environmental variables from different bracken management treatments.

Table S3. Correlations and variance explained (%) of 12 environmental variables.

Environmental variables	**Correlations**		**Variance explained**	
	Axis 1	**Axis 2**	**Axis 1**	**Axis 2**
pH	0.059	0.163	0.35	2.66
Potassium	-0.139	-0.050	1.94	0.25
Phosphorus	-0.027	-0.003	0.07	0.0002
Nitrogen	-0.168	-0.293	2.81	8.58
Carbon	-0.121	-0.347	1.45	12.03
Organic matter	-0.242	-0.200	5.85	4.00
PAR	0.408	0.025	16.61	0.02
Soil temperature	0.402	0.049	16.20	0.24
Litter depth	-0.411	0.421	16.90	17.72
Live bracken biomass	-0.419	-0.144	17.55	2.07
Dead bracken biomass	-0.349	0.572	12.15	32.73
Soil moisture	-0.285	-0.443	8.12	19.66

Table S4. Mean ± standard deviation of all environmental variables assessed in different treatments of bracken management and in forest interior. Bracken treatments are: with bracken fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOREST). PAR = Photosynthetically active radiation. Different letters in rows indicate significant ($p<0.05$) differences, based on an LMM and post hoc Tukey test.

Treatment/ Environmental variable	**F-L-**	**F-L+**	**F+L-**	**F+L+**	**FOREST**
pH	4.89±0.32a	4.94±0.22a	4.88±0.42a	4.89±0.49a	4.35±0.51b
Potassium	0.39±0.14a	0.38±0.16a	0.40±0.12a	0.51±0.20a	0.63±0.39a
Phosphorus	4.95±3.44a	4.00±1.95a	4.12±3.25a	5.72±4.52a	19.27±22.82b
Nitrogen	0.62±0.14a	0.71±0.25a	0.76±0.20a	0.80±0.28a	1.19±0.43b
Carbon	10.63±2.41a	12.18±3.85ab	12.12±3.00ab	12.10±3.68ab	17.49±7.66b
Organic matter	18.18±4.10a	20.90±6.57ab	20.75±5.37ab	20.95±6.50ab	30.06±13.44b
Soil temperature	22.64±2.47a	20.78±1.25b	18.47±1.79c	17.24±1.36d	17.15±1.04d
Soil moisture	33.93±5.31a	40.94±5.53a	41.09±4.67b	41.88±6.65c	42.65±5.45c
Dead bracken biomass	NA	707.19±265.98b	NA	1660.13±645.4a	NA
Alive bracken biomass	NA	NA	735.94±153.97a	775.63±316.96b	NA
Litter depth	NA	6.59±1.21a	NA	14.98±5.50b	8.51±1.31c
PAR	81.25±9.81a	78.32±13.92a	15.77±7.24b	1.71±0.79c	2.32±0.78c

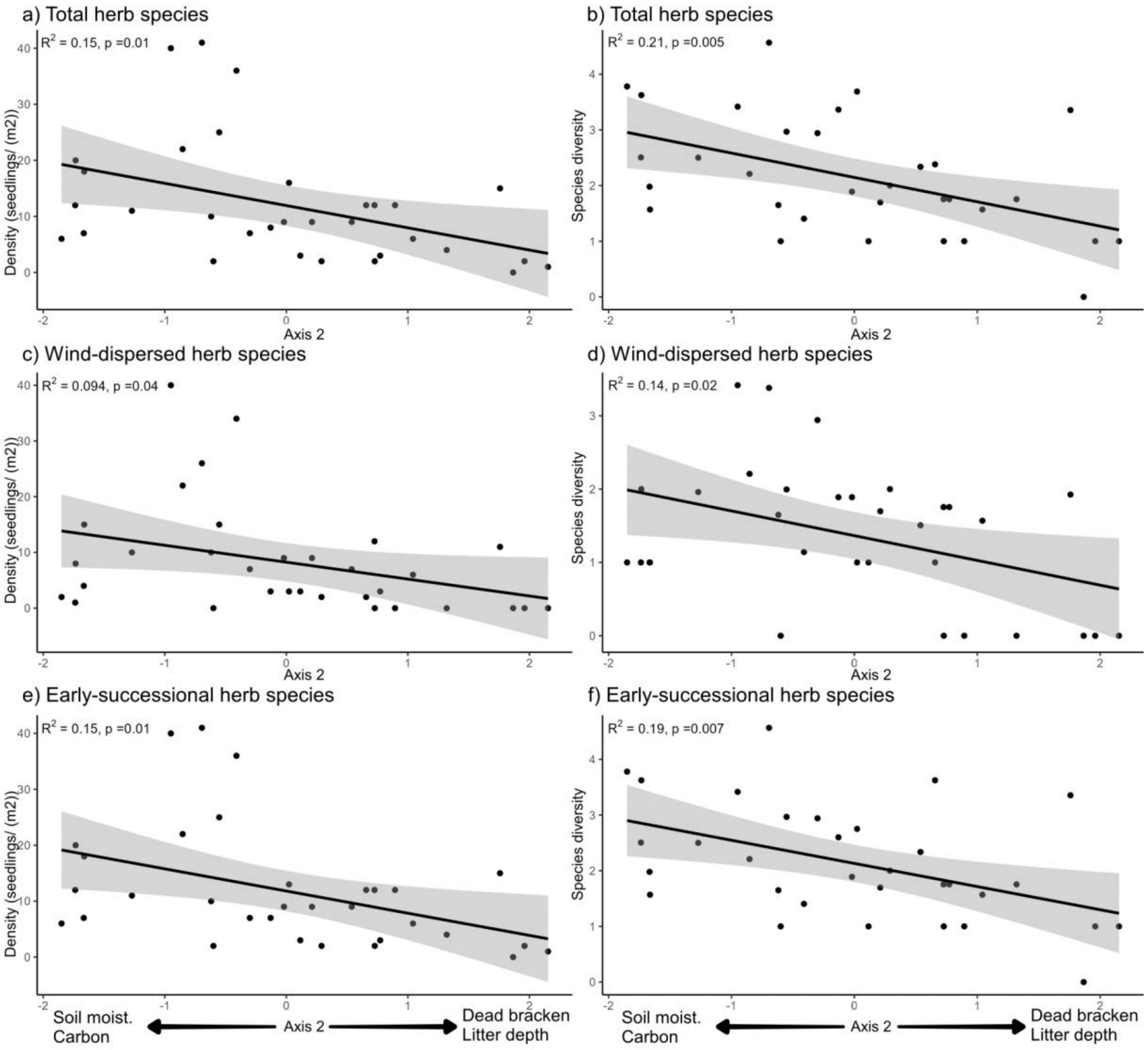


Figure S4. Significant regressions between environmental variables and Density and Species diversity of: (a) Tree species, (b) Animal-dispersed tree species, (c) Early-successional species and Density of: (d) Late-successional shrub species.

Supplementary Material Chapter III

Table S1. Seedling abundance found in the SSB in function of (a) life form and (b) dispersal syndrome.

	Total	Bracken	Forest
(a) All	3,177 (100%)	2,549 (80.23%)	628 (19.76%)
(b) Life form			
Herbs	1,802 (100%)	1,535 (85.18%)	267 (14.81%)
Shrubs	1,052 (100%)	909 (86.4%)	143 (13.59%)
Trees	323 (100%)	105 (32.5%)	218 (67.49%)
(c) Dispersal syndrome			
Anemochorous	2,712 (100%)	2,317 (85.4%)	395 (14.56%)
Zoochorous	465 (100%)	232 (49.89%)	233 (50.11%)

Table S2. Effect of *Pteridium* fronds (FR) and litter (LIT) on the soil seed bank in terms of (a) abundance, (b) richness and (c) diversity, from Generalized linear mixed effect models including site as a random effect. Only the variables included in the best models and null models are shown. P-values correspond to the likelihood-ratio test, significant values (p<0.05) are denoted in bold.

(a) Abundance	***df***	**AICc**	**Δ AICc**	**weight**	***R*²m**	***P***
All						
Null model	3	306.8	0	0.55	0	
FR	4	308.7	1.90	0.21	0.01	0.81
Trees						
Null model	3	154.5	0	0.56	0	
FR	4	156.4	1.9	0.22	0.04	0.78
Non-Trees						
Null model	3	308.1	0	0.57		
FR	4	310.2	2.13	0.19	0.01	0.48
Anemochorous						
Null model	3	305.9	0	0.60		
FR	4	308.3	2.46	0.17	0.003	0.68
Endozoochorous*						
FR	3	189.6	0	0.46	0.13	**0.03**
FR+LIT+FR:LIT	5	191.2	1.63	0.2		
Null model	2	191.7	2.09	0.12		
(b) Richness						
All						
FR+LIT	4	186.2	0	0.41	0.21	**0.01**
LIT	3	187	1.21	0.22		
FR+LIT+FR:LIT	5	187.7	1.57	0.18		
Null model	2	190.1	3.94	0.05		

Trees*						
LIT	2	97.5	0	0.60	0.16	**0.02**
Null model	1	100.8	3.27	0.11		
Non-Trees						
LIT	3	180	0	0.36	0.09	0.05
FR+LIT	4	180.8	0.81	0.24		
Null model	2	181.3	1.31	0.18		
Anemochorous						
LIT	3	180.2	0	0.48	0.1	**0.04**
Null model	2	181.9	1.8	0.19		
Endozoochorous*						
FR	2	111	0	0.54	0.17	**0.01**
FR+LIT	3	112.4	1.38	0.27		
Null model	1	114.9	3.92	0.08		
(c) Inverse Simpson Index						
All						
LIT	4	175.4	0	0.41	0.1	**0.04**
Null model	3	176.7	1.3	0.21		
Trees*						
FR+LIT	4	92.0	0	0.33	0.20	**0.03**
LIT	3	92.8	0.79	0.22		
FR	3	92.9	0.99	0.20		
Null model	2	93.6	1.61	0.15		
Non-Trees*						
LIT	3	160.4	0	0.48	0.12	**0.04**
Null model	2	162.1	1.73	0.2		
Anemochorous						
LIT	4	162	0	0.35	0.09	0.06
Null model	3	162.8	0.83	0.23		
Endozoochorous						
FR+LIT	5	89.1	0	0.44	0.22	**0.008**
FR	4	89.6	0.52	0.34		
Null model	3	93.3	4.22	0.05		

* Models analyzed with GLM

Table S3. List of species found in the soil seed bank.

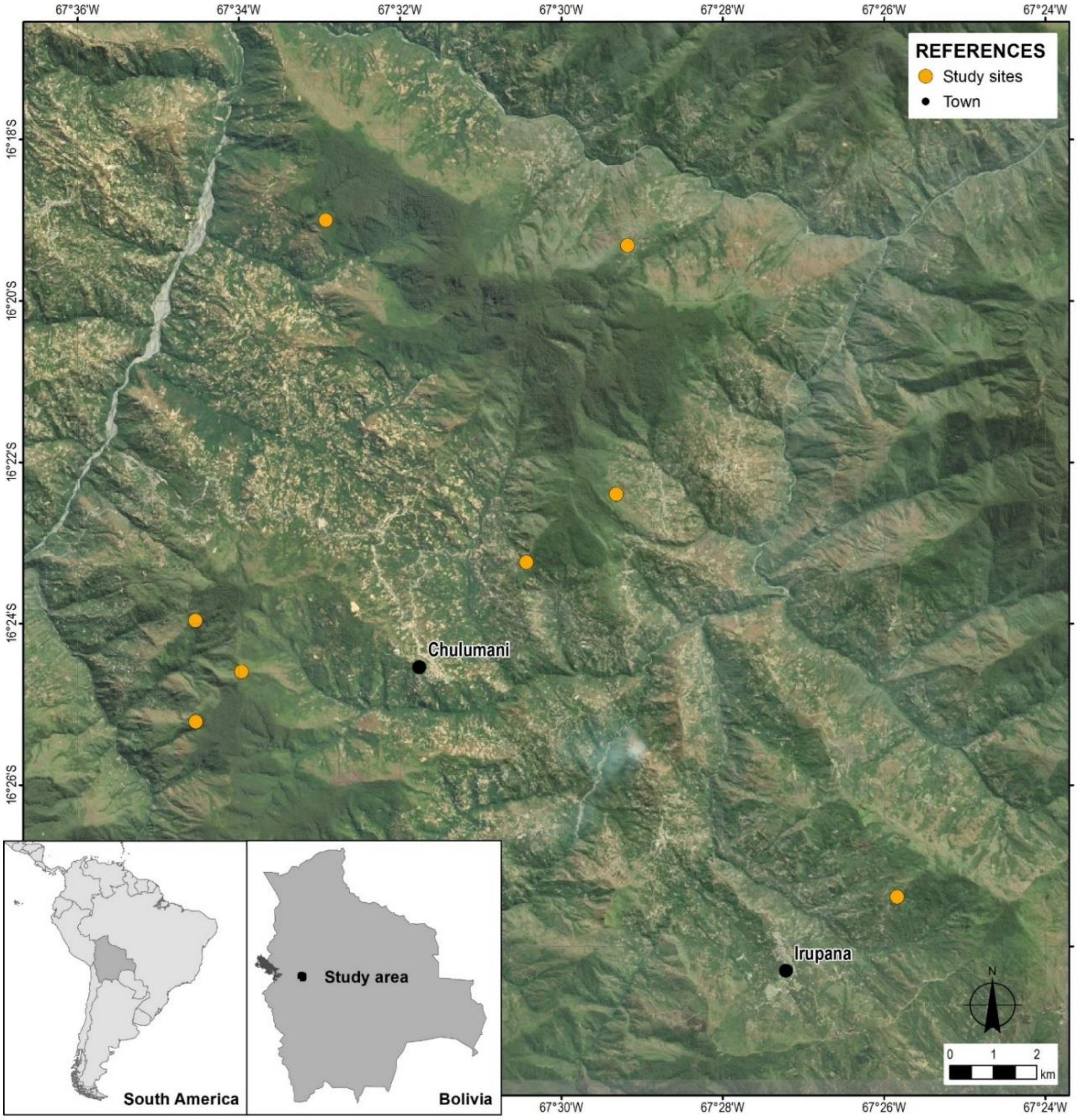
Family	**Specie**	**Life form**	**Dispersion symdrome**
Apocynaceae	*Blepharodon salicinum*	Herb	Anemochourus
Apocynaceae	*Mandevilla brachyloba*	Herb	Anemochourus
Araceae	Araceae sp EAJ 325	Herb	Zoochorous
Asteraceae	*Achyrocline alata*	Herb	Anemochourus
Asteraceae	*Achyrocline flaccida*	Herb	Anemochourus
Asteraceae	Asteraceae EAJ 123	Herb	Anemochourus
Asteraceae	Asteraceae EAJ 95	Herb	Anemochourus
Asteraceae	Asteraceae sp EAJ 125	Herb	Anemochourus
Asteraceae	Asteraceae sp EAJ 364	Herb	Anemochourus
Asteraceae	*Austroeupatorium inulifolium*	Shrub	Anemochourus
Asteraceae	*Baccharis dracunculifolia*	Shrub	Anemochourus
Asteraceae	*Baccharis latifolia*	Shrub	Anemochourus
Asteraceae	*Baccharis nitida*	Shrub	Anemochourus
Asteraceae	*Baccharis* sp EAJ 269	Shrub	Anemochourus
Asteraceae	*Baccharis trinervis var. debilis*	Herb	Anemochourus
Asteraceae	*Chaptalia integerrima*	Herb	Anemochourus
Asteraceae	*Chaptalia mandonii*	Herb	Anemochourus
Asteraceae	*Chaptalia nutans*	Herb	Anemochourus
Asteraceae	*Chaptalia* sp EAJ 260	Herb	Anemochourus
Asteraceae	*Chromolaena subscandens*	Shrub	Anemochourus
Asteraceae	*Chrysolaena obovata*	Herb	Anemochourus
Asteraceae	*Conyza primulifolia*	Herb	Anemochourus
Asteraceae	*Dendrophorbium biacuminatum*	Shrub	Anemochourus
Asteraceae	*Dendrophorbium multinerve*	Shrub	Anemochourus
Asteraceae	*Gamochaeta pensylvanica*	Herb	Anemochourus
Asteraceae	*Gnaphalium simplicicaule*	Herb	Anemochourus
Asteraceae	*Gnaphalium simplicicaule*	Herb	Anemochourus
Asteraceae	*Hieracium adenocephalum*	Herb	Anemochourus
Asteraceae	*Lepidaploa canescens*	Shrub	Anemochourus
Asteraceae	*Mikania baccharoidea*	Shrub	Anemochourus
Asteraceae	*Mikania longiacuminata*	Herb	Anemochourus
Asteraceae	*Mikania* sp EAJ 122	Herb	Anemochourus
Asteraceae	*Mikania* sp EAJ 243	Shrub	Anemochourus
Asteraceae	*Munnozia gigantea*	Shrub	Anemochourus
Asteraceae	*Munnozia* sp EAJ 70	Herb	Anemochourus
Asteraceae	*Ophryosporus kuntzei*	Herb	Anemochourus
Asteraceae	*Stevia boliviensis*	Herb	Anemochourus
Asteraceae	*Stevia glanduloso-pubescens*	Herb	Anemochourus
Asteraceae	*Stevia neglecta*	Herb	Anemochourus
Asteraceae	*Stevia* sp EAJ 169	Herb	Anemochourus
Asteraceae	*Stevia* sp EAJ 245	Herb	Anemochourus

Blechnaceae	*Blechnum* sp EAJ 175	Herb	Anemochourus
Anacardiaceae	*Mauria* sp EAJ 225	Tree	Zoochorous
Campanulaceae	*Siphocampylus* sp EAJ 193	Shrub	Anemochourus
Campanulaceae	*Siphocampylus* sp EAJ 63	Shrub	Anemochourus
Caryophyllaceae	*Arenaria lanuginosa*	Herb	Anemochourus
Caryophyllaceae	Caryophyllaceae sp EAJ 152	Herb	Anemochourus
Caryophyllaceae	*Paronychia setigera*	Herb	Anemochourus
Chloranthaceae	*Hedyosmum angustifolium*	Tree	Zoochorous
Clethraceae	*Clethra revoluta*	Tree	Anemochourus
Clethraceae	*Clethra scabra*	Tree	Anemochourus
Droseraceae	*Drosera montana*	Herb	Anemochourus
Euphorbiaceae	*Alchornea* sp. EAJ 62	Tree	Zoochorous
Euphorbiaceae	*Dysopsis glechomoides*	Herb	Anemochourus
Fabaceae	*Camptosema praeandinum*	Shrub	Anemochourus
Fabaceae	*Chamaecrista glandulosa*	Shrub	Anemochourus
Fabaceae	*Crotalaria nitens*	Shrub	Anemochourus
Gentianaceae	*Chelonanthus acutangulus*	Herb	Anemochourus
Gentianaceae	Gentianaceae sp EAJ 370	Herb	Anemochourus
Gentianaceae	*Macrocarpaea bangiana*	Herb	Anemochourus
Hypericaceae	*Vismia pozuzoensis*	Tree	Zoochorous
Indeterminate	sp1	Indet	Indet
Indeterminate	sp10	Indet	Indet
Indeterminate	sp11	Indet	Indet
Indeterminate	sp12	Indet	Indet
Indeterminate	sp13	Indet	Indet
Indeterminate	sp14	Indet	Indet
Indeterminate	sp15	Indet	Indet
Indeterminate	sp16	Indet	Indet
Indeterminate	sp17	Indet	Indet
Indeterminate	sp18	Indet	Indet
Indeterminate	sp19	Indet	Indet
Indeterminate	sp2	Indet	Indet
Indeterminate	sp20	Indet	Indet
Indeterminate	sp21	Indet	Indet
Indeterminate	sp22	Indet	Indet
Indeterminate	sp23	Indet	Indet
Indeterminate	sp24	Indet	Indet
Indeterminate	sp25	Indet	Indet
Indeterminate	sp26	Indet	Indet
Indeterminate	sp27	Indet	Indet
Indeterminate	sp29	Indet	Indet
Indeterminate	sp3	Indet	Indet
Lamiaceae	*Hyptis* sp 1	Shrub	Anemochourus

Lamiaceae	*Hyptis* sp 2	Shrub	Anemochourus
Lamiaceae	*Lepechinia graveolens*	Shrub	Anemochourus
Lamiaceae	*Lepechinia* sp EAJ 321	Shrub	Anemochourus
Lythraceae	*Cuphea cordata*	Herb	Anemochourus
Lythraceae	*Cuphea* sp EAJ 52	Herb	Anemochourus
Lythraceae	*Cuphea weddelliana*	Herb	Anemochourus
Malvaceae	*Sida rhombifolia*	Shrub	Anemochourus
Malvaceae	*Sida spinosa*	Shrub	Anemochourus
Melastomataceae	*Miconia cordata*	Shrub	Zoochorous
Melastomataceae	*Miconia cyanocarpa var. dendritica*	Shrub	Zoochorous
Melastomataceae	*Miconia cyanocarpa var hirsuta*	Shrub	Zoochorous
Melastomataceae	*Miconia cyanocarpa var parvifolia*	Shrub	Zoochorous
Melastomataceae	*Miconia hygrophila*	Shrub	Zoochorous
Melastomataceae	*Miconia leacrenata*	Shrub	Zoochorous
Melastomataceae	*Miconia* sp EAJ 178	Shrub	Zoochorous
Melastomataceae	*Miconia sublanata*	Shrub	Zoochorous
Melastomataceae	*Miconia theaezans*	Tree	Zoochorous
Melastomataceae	*Chaetogastra brittoniana*	Shrub	Anemochourus
Melastomataceae	*Chaetogastra citrina*	Shrub	Anemochourus
Melastomataceae	*Chaetogastra confertiflora*	Shrub	Anemochourus
Melastomataceae	*Chaetogastra longifolia*	Shrub	Anemochourus
Melastomataceae	*Pleroma stenocarpum*	Shrub	Anemochourus
Myricaceae	*Morella pubescens*	Tree	Zoochorous
Oxalidaceae	*Oxalis spiralis*	Herb	Anemochourus
Oxalidaceae	*Oxalis* sp	Herb	Anemochourus
Phyllanthaceae	*Hieronyma fendleri var. boliviensis*	Tree	Zoochorous
Phyllanthaceae	*Phyllanthus* sp EAJ 172	Tree	Zoochorous
Piperaceae	*Piper bolivianum*	Tree	Zoochorous
Piperaceae	*Piper oxyphyllum*	Shrub	Zoochorous
Poaceae	Poaceae sp 1	Herb	Anemochourus
Poaceae	Poaceae sp 2	Herb	Anemochourus
Poaceae	Poaceae sp 3	Herb	Anemochourus
Poaceae	Poaceae sp 4	Herb	Anemochourus
Poaceae	Poaceae sp 5	Herb	Anemochourus
Poaceae	Poaceae sp 6	Herb	Anemochourus
Primulaceae	*Myrsine coriácea*	Tree	Zoochorous
Pteridaceae	Pteridaceae sp EAJ 208	Herb	Anemochourus
Pteridaceae	*Selaginella* sp EAJ 289	Herb	Anemochourus
Rubiaceae	*Borreria lanceolata*	Herb	Anemochourus
Rubiaceae	*Galium hypocarpium*	Herb	Zoochorous
Rubiaceae	*Galium noxium*	Herb	Zoochorous
Rubiaceae	*Galium* sp EAJ 176	Herb	Zoochorous
Rubiaceae	*Notopleura* sp EAJ 133	Shrub	Zoochorous

Rubiaceae	*Randia* sp EAJ 249	Tree	Zoochorous
Sapindaceae	Sapindaceae sp EAJ 262	Shrub	Zoochorous
Smilacaceae	*Smilax* sp EAJ 195	Herb	Zoochorous
Solanaceae	*Solanum palinacanthum*	Shrub	Zoochorous
Urticaceae	*Cecropia elongata*	Tree	Zoochorous
Urticaceae	*Myriocarpa stipitata*	Tree	Zoochorous
Violaceae	*Viola boliviana*	Herb	Anemochourus

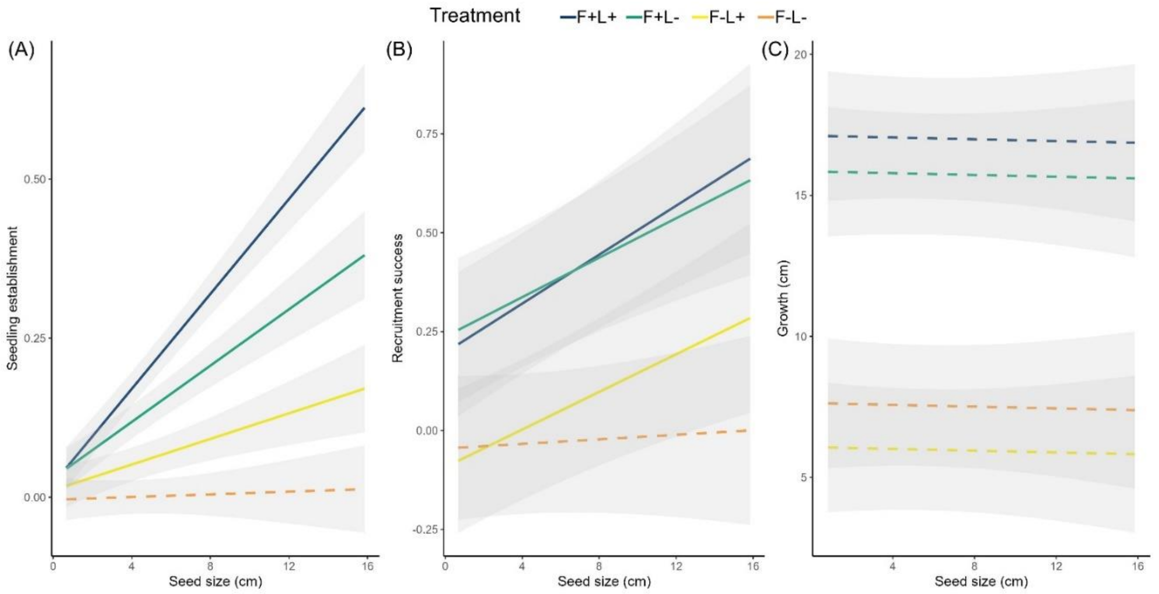
Supplementary material chaper IV



Supplementary Figure 1. Map of the study area in Sud Yungas, La Paz, Bolivia. The eight study sites were stablished at 100 m from the forest borders.

Supplementary Table 1. Detail of families, number of seeds sown per sub-quadrant and mean ± standard deviation of seed size (i.e. seed length) of the 24 tree species used in the seed addition experiment. Species used for transplanting are marked with an asterisk (*).

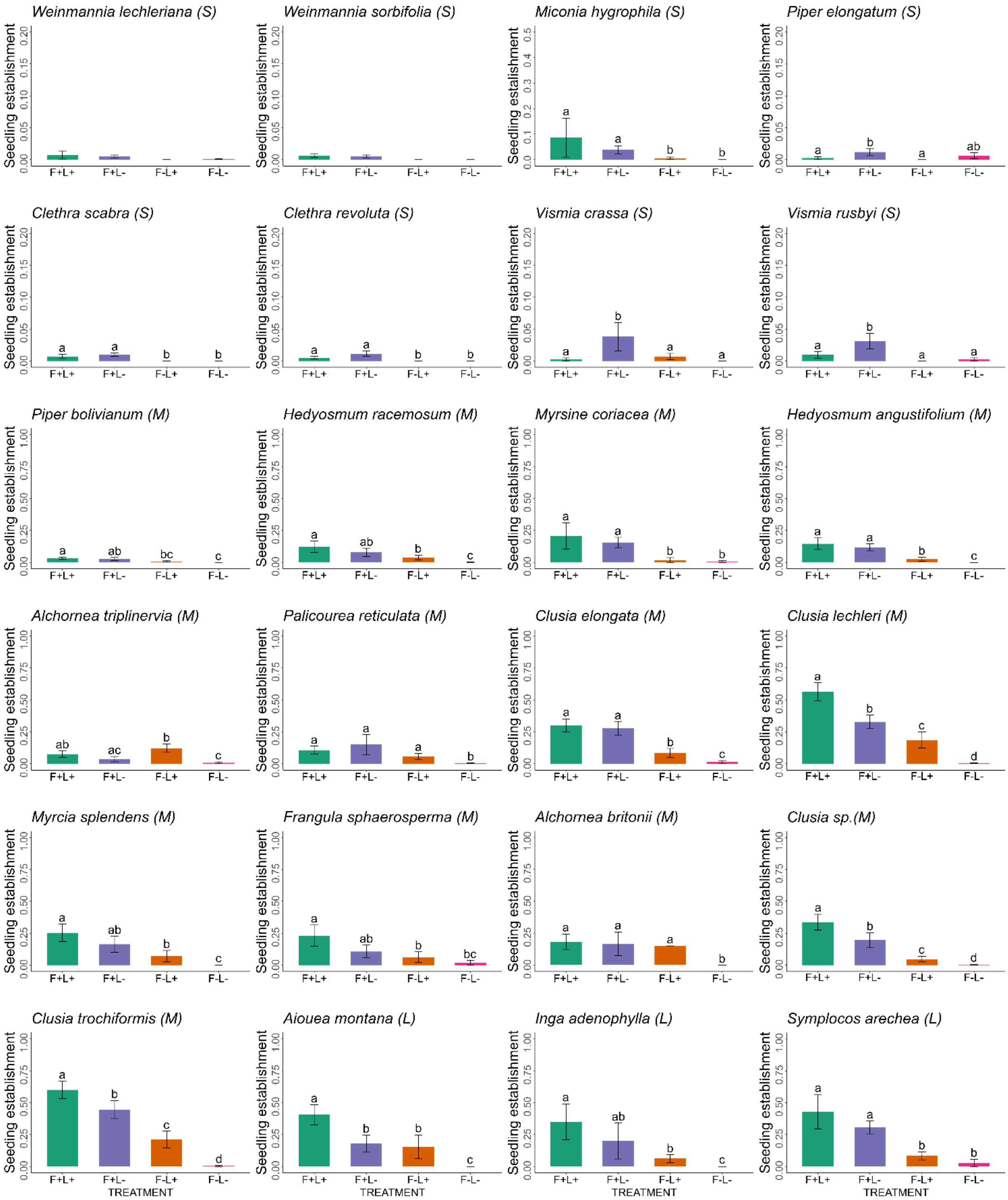
Family	Specie	# of seeds sown	Seed size (mm) ± SD
Cunnoniaceae	Weinmannia lechleriana Engl.	50	0.68±0.11
Cunnoniaceae	Weinmannia sorbifolia Kunth	50	0.73±0.08
Melastomataceae	Miconia hygrophila Naudin *	50	0.83±0.21
Piperaceae	Piper elongatum Vahl	20	0.93±0.11
Clethraceae	Clethra scabra Pers.	50	1.15±0.21
Clethraceae	Clethra revoluta (Ruiz & Pav.) Spreng.	50	1.44±0.20
Hypericaceae	Vismia rusbyi Ewan *	15	1.84±0.22
Hypericaceae	Vismia crassa (Rusby) Blake *	15	1.85±0.12
Piperaceae	Piper bolivianum C. DC. *	20	2.39±0.13
Chlorantaceae	Hedyosmum racemosum (Ruiz & Pav.) G. Don *	15	2.83±0.24
Primulaceae	Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult. *	10	3.34±0.14
Chlorantaceae	Hedyosmum angustifolium (Ruiz & Pavon) Solms-Laubach	10	3.42±0.21
Euphorbiaceae	Alchornea triplinervia (Sprengel) Muell.-Arg.	10	3.73±0.39
Rubiaceae	Palicourea reticulata (Ruiz & Pav.) C.M, Taylor	10	3.82±0.37
Clusiaceae	Clusia elongata Rusby *	10	4.81±0.73
Myrtaceae	Myrcia splendens (Sw.) DC. aff.	5	4.96±0.62
Clusiaceae	Clusia lechleri Rusby *	10	5.1±0.71
Rhamnaceae	Rhamnus sphaerosperma (Sw.) Kartesz & Gandhi *	10	5.35±0.31
Euphorbiaceae	Alchornea brittonii Secco	5	5.59±0.55
Clusiaceae	Clusia sp. *	10	5.65±0.37
Clusiaceae	Clusia trochiformis Vesque *	10	6.07±0.67
Lauraceae	Aiouea montana (Sw.) R. Rohde *	3	11.11±1.22
Euphorbiaceae	Inga adenophylla Pittier *	5	12±1.14
Symplocaceae	Symplocos arechea L´Herit. *	3	15.85±1.30



Supplementary Figure 2. Relationship between seed size and (A) seedling establishment, (B) recruitment success, and (C) growth in four treatments, represented by different colors. Treatments are denoted as follows: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. GLMM model trendlines are shown with 95% confidence intervals (gray shading), with solid lines indicating significant and dashed lines representing non-significant effects of seed size on seedling performance for each treatment.

Supplementary Table 2. Generalized linear mixed effects models (GLMM) for the effect of seed size on a) Seedling establishment, b) Recruitment success and c) Growth, for each treatment analyzed separately. The intercept was set to zero to facilitate comparison. P-values <0.05 are denoted in bold.

	Estimate	Std. Error	Z value	p-value	LRT test p-value	R2 marginal
a) Seedling establishment						
F+L+	0.24	0.02	8.02	**<0.001**	**<0.001**	0.64
F+L-	0.16	0.03	4.44	**<0.01**	**<0.001**	0.59
F-L+	0.21	0.03	6.56	**<0.001**	**<0.001**	0.52
F-L-	0.51	0.65	0.78	0.43	0.19	0.17
b) Recruitment success						
F+L+	0.04	0.08	4.44	**<0.001**	**<0.001**	0.38
F+L-	0.07	0.02	2.64	**<0.01**	**<0.01**	0.35
F-L+	0.02	0.03	6.66	**<0.001**	**<0.001**	0.21
F-L-	0.004	0.003	1.35	0.17	0.23	0.08
c) Growth						
F+L+	0.04	0.23	0.19	0.84	0.68	0.21
F+L-	0.01	0.20	0.06	0.94	0.66	0.18
F-L+	0.07	0.12	0.55	0.57	0.57	0.21
F-L-	0.01	0.12	0.12	0.90	0.90	0.12



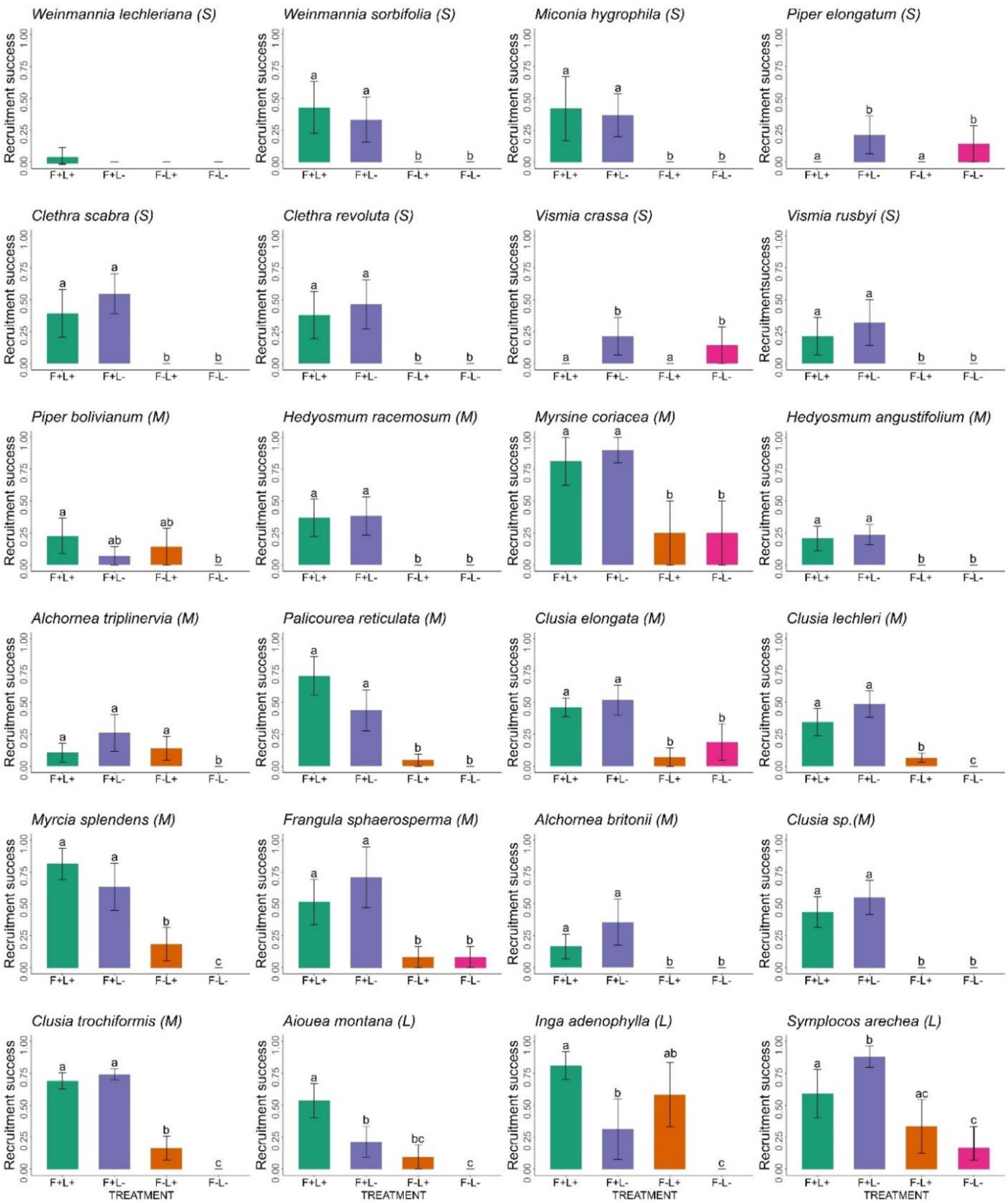
Supplementary Figure 3. Proportion of seedlings established in experimental bracken management treatments for each sown species. Treatments are denoted as follows: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots show predicted values from the generalized linear mixed-effects models (GLMMs) ± SE. Different letters indicate significant differences between treatments at the 0.05 level, as determined by post hoc Tukey tests. Species are arranged from small-seeded species at the top to large-seeded species at the bottom, with seed size categories indicated in parentheses: (S) small, (M) medium, and (L) large. Note that the Y-axis scales differ across plots.

Supplementary Table 3. Generalized Linear Mixed Effects Models (GLMM) for seedling establishment of each species in response to treatment. Treatment with fronds and litter present (F+L+) is in the intercept. P-values <0.05 are denoted in bold. Species are arranged from small-seeded species at the top to large-seeded species at the bottom, with seed size categories indicated in parentheses: (S) small, (M) medium, and (L) large.

	Estimate	**Std. Error**	**Z value**	**p-value**	**LRT test p-value**	**R2 marginal**
Weinmannia lechleriana (S)						
Intercept	-16.12	0.73	-7.54	**<0.001**	**<0.001**	0.66
F+L-	-0.06	0.85	-0.71	0.67		
F-L+	-0.09	0.86	-0.73	0.49		
F-L-	-0.98	2.24	-0.80	0.92		
Weinmania sorbifolia (S)						
Intercept	-17.74	0.11	-15.08	**<0.001**	**<0.001**	0.45
F+L-	-0.07	0.14	-0.50	0.23		
F-L+	-0.07	0.17	-0.40	0.68		
F-L-	-0.13	0.21	-0.43	0.71		
Miconia hygrophila (S)						
Intercept	-3.31	0.97	-3.41	**<0.001**	**<0.001**	0.64
F+L-	-0.86	0.60	-1.43	0.15		
F-L+	-2.74	0.96	-2.84	**<0.01**		
F-L-	-3.49	1.45	-3.04	**<0.01**		
Piper elongatum (S)						
Intercept	-6.04	1.02	-5.89	**<0.001**	**<0.05**	0.98
F+L-	-0.09	0.25	-0.61	0.42		
F-L+	-11.09	0.75	-7.23	**<0.001**		
F-L-	-21.42	0.23	-5.34	**<0.001**		
Clethra scabra (S)						
Intercept	-18.74	0.41	-12.12	**<0.001**	**<0.001**	0.45
F+L-	-0.07	0.52	0.88	0.61		
F-L+	-10.09	0.16	-6.02	**<0.001**		
F-L-	-26.43	0.28	-9.43	**<0.001**		
Clethra revoluta (S)						
Intercept	-12.43	0.56	-15.08	**<0.001**	**<0.001**	0.66
F+L-	-0.83	0.45	1.83	-0.08		
F-L+	-6.29	0.75	-7.79	**<0.001**		
F-L-	-21.66	0.22	-8.21	**<0.001**		
Vismia crassa (S)						
Intercept	-6.71	1.16	-5.78	**<0.001**	**<0.001**	0.93
F+L-	2.86	1.03	2.76	**<0.01**		
F-L+	1.11	1.16	1.77	0.33		

F-L-	-19.65	1.84	-8.11	0.99		
Vismia rusbyi (S)						
Intercept	-4.76	1.93	-2.84	**<0.001**	**<0.001**	0.98
F+L-	1.20	1.24	2.76	**<0.05**		
F-L+	-5.72	1.64	-1.79	0.73		
F-L-	-13.94	6.84	-8.39	0.99		
Piper bolivianum (M)						
Intercept	-3.30	0.34	-9.58	**<0.001**	**<0.001**	0.66
F+L-	-0.43	0.54	-0.79	0.43		
F-L+	-1.66	0.77	-2.14	**<0.05**		
F-L-	-2.28	1.97	-3.44	**<0.05**		
Hedyousmum racemosum (M)						
Intercept	-17.78	0.39	-5.77	**<0.001**	**<0.001**	0.79
F+L-	-0.48	0.31	-1.57	0.06		
F-L+	-9.24	0.38	-3.44	**<0.001**		
F-L-	-15.09	6.58	-3.69	**<0.001**		
Myrsine coriacea (M)						
Intercept	-1.40	0.30	-4.57	**<0.001**	**<0.001**	0.83
F+L-	-0.34	0.29	-1.17	0.24		
F-L+	-2.64	0.61	-4.28	**<0.001**		
F-L-	-3.75	1.02	-3.67	**<0.001**		
Hedyosmum angustifolium (M)						
Intercept	-1.85	0.32	-5.67	**<0.001**	**<0.05**	0.91
F+L-	-0.14	0.41	-0.34	0.99		
F-L+	-1.38	0.72	-2.87	**<0.01**		
F-L-	-2.03	0.84	-4.34	**<0.01**		
Alchornea triplinervia (M)						
Intercept	-2.53	0.38	-6.61	**<0.001**	**<0.001**	0.68
F+L-	-0.89	0.66	-1.35	0.17		
F-L+	1.14	0.48	1.23	0.21		
F-L-	-2.36	1.07	-2.20	**<0.05**		
Palicourea reticulata (M)						
Intercept	-2.25	0.51	-4.40	**<0.001**	**<0.05**	0.61
F+L-	0.16	0.47	0.35	0.72		
F-L+	-0.83	0.52	-1.60	0.10		
F-L-	-3.13	1.07	-2.92	**<0.01**		
Clusia elongata (M)						
Intercept	0.86	0.23	3.59	**<0.001**	**<0.001**	0.66
F+L-	-0.09	0.33	-0.27	0.78		
F-L+	-1.50	0.43	-3.44	**<0.001**		
F-L-	-3.23	0.76	-2.23	**<0.05**		
Clusia lechleri (M)						
Intercept	0.26	0.28	0.92	**<0.001**	**<0.05**	0.78

F+L-	-0.95	0.36	-2.59	**<0.01**		
F-L+	-9.58	0.42	-4.60	**<0.001**		
F-L-	-2.10	5.77	-4.73	**<0.001**		
Myrcia splendens (M)						
Intercept	-1.77	0.11	-15.08	**<0.001**	**<0.001**	0.91
F+L-	-0.07	0.14	-0.50	0.61		
F-L+	-1.09	0.16	-4.02	**<0.001**		
F-L-	-2.64	0.28	-5.43	**<0.001**		
Frangula sphaerosperma (M)						
Intercept	-1.57	0.77	-2.03	**<0.05**	**<0.001**	0.47
F+L-	-0.95	0.57	-1.66	0.09		
F-L+	-1.78	0.73	-2.43	**<0.05**		
F-L-	-2.90	1.02	-2.82	**<0.01**		
Alchornea britonii (M)						
Intercept	-1.49	0.35	-4.19	**<0.001**	**<0.001**	0.84
F+L-	-0.13	0.52	-0.26	0.79		
F-L+	-0.22	0.52	-0.42	0.67		
F-L-	-6.21	1.36	-1.02	**<0.05**		
Clusia sp. (M)						
Intercept	-0.88	0.45	-1.92	**<0.05**	**<0.05**	0.66
F+L-	-0.79	0.32	-2.45	**<0.01**		
F-L+	-2.63	0.52	-5.01	**<0.001**		
F-L-	-4.62	1.06	-4.34	**<0.001**		
Clusia trochiformis (M)						
Intercept	0.39	0.27	1.42	**<0.001**	**<0.001**	0.57
F+L-	-6.49	0.38	-3.58	**<0.05**		
F-L+	-1.82	0.43	-4.16	**<0.001**		
F-L-	-5.04	1.06	-4.73	**<0.001**		
Aiouea montana (L)						
Intercept	-0.43	0.23	-1.94	**<0.05**	**<0.001**	0.94
F+L-	-2.48	0.52	-3.38	**<0.001**		
F-L+	-1.56	0.56	-2.18	**<0.05**		
F-L-	-2.34	0.87	-4.11	**<0.001**		
Inga adenophylla (L)						
Intercept	-0.61	0.53	-1.14	0.25	**<0.001**	0.64
F+L-	-1.17	0.84	-1.39	0.16		
F-L+	-1.91	0.85	-2.17	**<0.05**		
F-L-	-3.12	1.06	-3.02	**<0.05**		
Symplocos arechea (L)						
Intercept	-0.32	0.36	-0.89	**<0.001**	**<0.001**	0.83
F+L-	-0.43	0.51	-0.83	0.40		
F-L+	-1.81	0.64	-2.82	**<0.05**		
F-L-	-3.31	1.07	-3.08	**<0.05**		



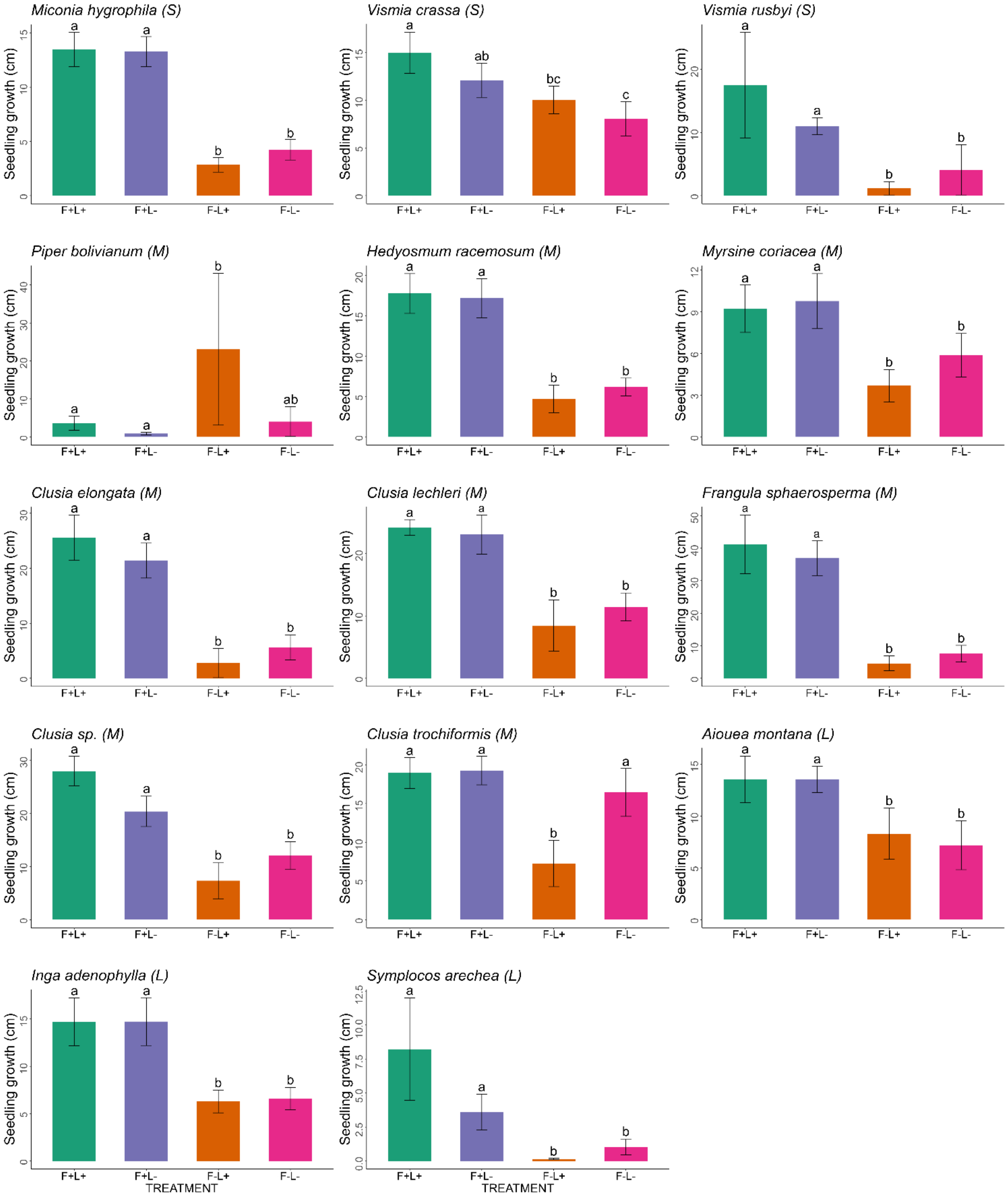
Supplementary Figure 4. Proportion of recruitment success of each species sown in experimental bracken management treatments were: (F+) represent bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots represent predicted fit values from the generalized linear mixed-effects models (GLMMs) ± SE. Different letters indicate significant differences between treatments at the 0.05 level, as determined by post hoc Tukey tests. Species are arranged from small-seeded species at the top to large-seeded species at the bottom, with seed size categories indicated in parentheses: (S) small, (M) medium, and (L) large.

Supplementary Table 4. Generalized Linear Mixed Effects Models (GLMM) for recruitment success of each species in response to treatment. Treatment with fronds and litter present (F+L+) is in the intercept. P-values <0.05 are denoted in bold. Species are arranged from small-seeded species at the top to large-seeded species at the bottom, with seed size categories indicated in parentheses: (S) small, (M) medium, and (L) large.

	Estimate	**Std. Error**	**Z value**	**p-value**	**LRT test p-value**	**R2 marginal**
Weinmannia lechleriana (S)						
Intercept	0.49	0.99	-0.49	0.61	**<0.001**	0.66
F+L-	-0.96	0.85	-1.13	0.25		
F-L+	-0.64	1.03	-0.62	0.53		
F-L-	-0.25	1.00	-0.25	0.79		
Weinmania sorbifolia (S)						
Intercept	0.08	0.08	1.04	0.31	**<0.001**	0.62
F+L-	0.13	0.11	1.14	0.25		
F-L+	-0.47	0.15	-3.08	**<0.01**		
F-L-	-0.45	0.17	-2.64	**<0.01**		
Miconia hygrophila (S)						
Intercept	4.37	0.74	5.87	**<0.001**	**<0.001**	0.87
F+L-	-0.43	0.32	-1.33	0.180		
F-L+	-1.56	0.19	-8.19	**<0.001**		
F-L-	-4.37	0.74	-5.87	**<0.001**		
Piper elongatum (S)						
Intercept	-0.14	0.14	-0.99	**<0.001**	**<0.001**	0.62
F+L-	0.91	0.31	2.87	**<0.01**		
F-L+	-12.44	0.26	-3.60	0.18		
F-L-	0.78	0.48	1.60	**<0.001**		
Clethra scabra (S)						
Intercept	-1.03	0.43	-2.39	**<0.01**	**<0.001**	0.84
F+L-	0.99	1.13	0.87	0.379		
F-L+	-2.02	0.97	-2.08	**<0.05**		
F-L-	-2.44	0.41	-5.94	**<0.001**		
Clethra revoluta (S)						
Intercept	-1.47	0.55	-2.65	**<0.01**	**<0.001**	0.64
F+L-	3.29	0.63	5.15	0.66		
F-L+	-0.76	0.45	-1.66	**<0.05**		
F-L-	-0.87	0.49	-1.21	**<0.05**		
Vismia crassa (S)						
Intercept	-1.79	1.08	-1.65	**<0.05**	**<0.001**	0.48
F+L-	0.16	0.06	2.57	**<0.05**		
F-L+	-0.69	0.70	-0.98	0.327		
F-L-	2.07	1.00	3.09	**<0.05**		

Vismia rusbyi (S)						
Intercept	-1.03	0.43	-2.39	**<0.05**	**<0.001**	0.56
F+L-	0.99	1.13	0.87	0.379		
F-L+	-2.02	0.97	-2.08	**<0.05**		
F-L-	-1.60	0.77	-2.07	**<0.05**		
Piper bolivianum (M)						
Intercept	2.63	0.41	6.29	**<0.001**	**<0.001**	0.42
F+L-	-0.98	1.22	-0.80	0.42		
F-L+	-0.37	0.59	-0.62	0.53		
F-L-	-1.17	0.61	-1.95	**<0.05**		
Hedyousmum racemosum (M)						
Intercept	-0.98	0.57	-1.69	**<0.05**	**<0.001**	0.92
F+L-	1.17	1.00	1.16	0.24		
F-L+	-0.79	0.30	-2.62	**<0.001**		
F-L-	-0.99	0.30	-3.26	**<0.001**		
Myrsine coriacea (M)						
Intercept	-1.46	1.28	-1.13	**<0.001**	**<0.001**	0.73
F+L-	2.36	1.40	-1.68	0.24		
F-L+	-2.56	0.82	-3.10	**<0.01**		
F-L-	-3.26	1.22	-4.17	**<0.001**		
Hedyosmum angustifolium (M)						
Intercept	-1.29	0.66	-1.95	**<0.05**	**<0.001**	0.86
F+L-	0.55	0.91	0.60	0.545		
F-L+	-2.02	0.97	-2.08	**<0.05**		
F-L-	-0.64	0.26	-2.39	**<0.05**		
Alchornea triplinervia (M)						
Intercept	-1.53	0.65	-2.32	**<0.05**	**<0.001**	0.97
F+L-	1.62	0.98	1.64	0.09		
F-L+	-0.19	0.87	-0.22	0.82		
F-L-	-19.05	2.27	-2.10	**<0.05**		
Palicourea reticulata (M)						
Intercept	0.88	0.83	1.06	0.28	**<0.05**	0.46
F+L-	-3.13	1.12	-1.08	**<0.05**		
F-L+	-3.88	1.95	-1.98	**<0.05**		
F-L-	-21.59	9.77	-3.20	**<0.05**		
Clusia elongata (M)						
Intercept	-1.77	0.59	-2.98	**<0.001**	**<0.001**	0.66
F+L-	0.43	0.32	1.33	0.18		
F-L+	-1.03	0.43	-2.39	**<0.05**		
F-L-	-1.03	0.43	-2.38	**<0.05**		
Clusia lechleri (M)						
Intercept	-0.83	0.50	-1.65	0.09	**<0.05**	0.92
F+L-	0.78	0.31	1.61	0.09		

F-L+	-1.36	0.49	-2.76	**<0.01**		
F-L-	-1.92	1.50	-2.81	**<0.01**		
Myrcia splendens (M)						
Intercept	1.12	0.22	4.95	**<0.001**	**<0.001**	0.62
F+L-	-0.19	0.16	-1.18	0.23		
F-L+	-0.55	0.24	-2.25	**<0.01**		
F-L-	-0.33	0.16	-2.05	**<0.01**		
Frangula sphaerosperma (M)						
Intercept	0.86	0.35	2.39	**<0.01**	**<0.001**	0.92
F+L-	1.92	1.09	1.75	0.079		
F-L+	-3.07	1.11	-2.74	**<0.01**		
F-L-	-2.15	1.27	-1.91	**<0.05**		
Alchornea britonii (M)						
Intercept	0.47	0.15	3.08	**<0.01**	**<0.001**	0.68
F+L-	0.78	0.97	0.80	0.423		
F-L+	-0.64	0.26	-2.39	**<0.01**		
F-L-	-0.91	0.29	-3.09	**<0.01**		
Clusia sp. (M)						
Intercept	1.56	0.19	8.19	**<0.001**	**<0.05**	0.87
F+L-	0.07	0.21	0.32	0.741		
F-L+	-0.73	0.23	-3.10	**<0.01**		
F-L-	-0.68	0.23	-2.91	**<0.01**		
Clusia trochiformis (M)						
Intercept	0.82	0.29	2.77	**<0.001**	**<0.001**	0.89
F+L-	0.25	0.35	0.59	0.55		
F-L+	-2.43	0.45	-4.29	**<0.001**		
F-L-	-12.40	1.67	-3.10	**<0.001**		
Aiouea montana (L)						
Intercept	2.20	0.33	6.60	**<0.001**	**<0.001**	0.62
F+L-	-1.28	0.63	-2.00	**<0.01**		
F-L+	-0.76	0.45	-1.66	**<0.01**		
F-L-	-0.36	0.15	-2.25	**<0.05**		
Inga adenophylla (L)						
Intercept	0.80	0.27	2.90	**<0.01**	**<0.001**	0.45
F+L-	-0.85	0.42	-1.98	**<0.01**		
F-L+	-0.70	0.42	-1.65	0.09		
F-L-	-0.76	0.45	-1.66	**<0.05**		
Symplocos arechea (L)						
Intercept	-1.35	0.61	-2.20	**<0.01**	**<0.001**	0.93
F+L-	0.66	0.26	2.50	**<0.01**		
F-L+	-1.35	1.03	-1.30	0.190		
F-L-	-0.64	0.26	-2.39	**<0.01**		



Supplementary Figure 5. Growth of transplanted seedlings in experimental bracken management treatments were: (F+) represent bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots represent predicted values from the generalized linear mixed-effects models (GLMMs) ± SE. Different letters indicate significant differences at level 0.05 based on post hoc Tukey tests. Species are arranged from small-seeded at the top to large-seeded at the bottom. Note that different scales in the Y axis are used.

Supplementary Table 5. Generalized Linear Mixed Effects Models (GLMM) for seedling growth of each species in response to treatment. Treatment with fronds and litter present (F+L+) is in the intercept. P-values <0.05 are denoted in bold. Species are arranged from small-seeded species at the top to large-seeded species at the bottom, with seed size categories indicated in parentheses: (S) small, (M) medium, and (L) large.

	Estimate	**Std. Error**	**Z value**	**p-value**	**LRT test p-value**	**R2 marginal**
Miconia hygrophila (S)						
Intercept	1.34	1.50	8.94	**<0.001**	**<0.001**	0.54
F+L-	-0.19	1.28	-0.12	0.42		
F-L+	-1.32	1.52	-6.95	**<0.001**		
F-L-	-9.24	1.45	-6.04	**<0.001**		
Vismia crassa (S)						
Intercept	1.49	1.67	7.36	**<0.001**	**<0.05**	0.61
F+L-	-2.89	2.37	-1.21	0.23		
F-L+	-4.95	2.12	-2.08	**<0.01**		
F-L-	-6.93	1.23	-2.92	**<0.01**		
Vismia rusbyi (S)						
Intercept	1.75	1.50	8.94	**<0.001**	**<0.05**	0.54
F+L-	-6.51	1.28	-0.12	0.42		
F-L+	-1.63	1.52	-6.95	**<0.001**		
F-L-	-7.49	1.45	-6.04	**<0.001**		
Piper bolivianum (M)						
Intercept	3.62	0.71	0.50	0.6157	**<0.05**	0.46
F+L-	-2.75	0.71	-0.29	0.7659		
F-L+	9.42	1.22	2.10	**<0.05**		
F-L-	0.42	1.29	0.04	0.9633		
Hedyosmum racemosum (M)						
Intercept	1.77	1.85	9.57	**<0.001**	**<0.05**	0.61
F+L-	-0.57	0.28	-0.26	0.79		
F-L+	-13.05	0.35	-5.98	**<0.001**		
F-L-	-11.56	0.30	-5.29	**<0.001**		
Myrsine coriacea (M)						
Intercept	9.22	1.65	5.57	**<0.001**	**<0.05**	0.69
F+L-	0.55	0.21	0.24	0.80		
F-L+	-5.54	0.25	-2.49	**<0.05**		
F-L-	-4.98	0.32	-2.86	**<0.05**		
Clusia elongata (M)						
Intercept	2.54	2.80	9.11	**<0.001**	**<0.001**	0.72
F+L-	-4.13	0.74	-1.12	0.26		
F-L+	-2.79	0.66	-6.17	**<0.001**		
F-L-	-1.91	0.63	-5.40	**<0.001**		

Clusia lechleri (M)						
Intercept	4.29	2.66	9.06	**<0.001**	**<0.001**	0.63
F+L-	-1.14	0.52	-0.35	0.72		
F-L+	-5.71	0.56	-4.86	**<0.001**		
F-L-	-7.27	0.57	-3.93	**<0.001**		
Frangula sphaerosperma (M)						
Intercept	4.11	0.39	8.05	**<0.001**	**<0.001**	0.61
F+L-	-4.23	0.45	-0.81	0.41		
F-L+	-3.55	0.43	-7.02	**<0.001**		
F-L-	-3.65	0.67	-6.44	**<0.001**		
Clusia sp. (M)						
Intercept	7.92	0.5	10.33	**<0.001**	**<0.001**	0.55
F+L-	-5.57	0.67	-0.87	0.06		
F-L+	-3.21	0.6	-5.41	**<0.001**		
F-L-	-8.51	0.84	-4.16	**<0.001**		
Clusia trochiformis (M)						
Intercept	9.86	0.46	8.06	**<0.001**	**<0.001**	0.54
F+L-	0.30	0.76	0.10	0.91		
F-L+	-11.70	0.57	-4.06	**<0.001**		
F-L-	-2.52	0.94	-0.87	0.38		
Aiouea montana (L)						
Intercept	13.52	0.5	6.83	**<0.001**	**<0.05**	0.54
F+L-	0.27	0.67	0.07	0.99		
F-L+	-6.01	0.6	-3.152	**<0.05**		
F-L-	-6.35	0.84	-2.304	**<0.05**		
Inga adenophylla (L)						
Intercept	14.72	1.74	7.18	**<0.001**	**<0.001**	0.57
F+L-	0.21	1.21	0.17	**0.42**		
F-L+	-8.43	0.99	-3.13	**<0.001**		
F-L-	-8.12	1.36	-3.02	**<0.001**		
Symplocos arechea (L)						
Intercept	8.22	1.84	4.46	**<0.001**	**<0.05**	0.49
F+L-	-4.63	2.29	-1.79	**0.42**		
F-L+	-8.07	1.26	-3.12	**<0.001**		
F-L-	-7.23	1.31	-2.78	**<0.001**		

Supplemantary material Chapter V

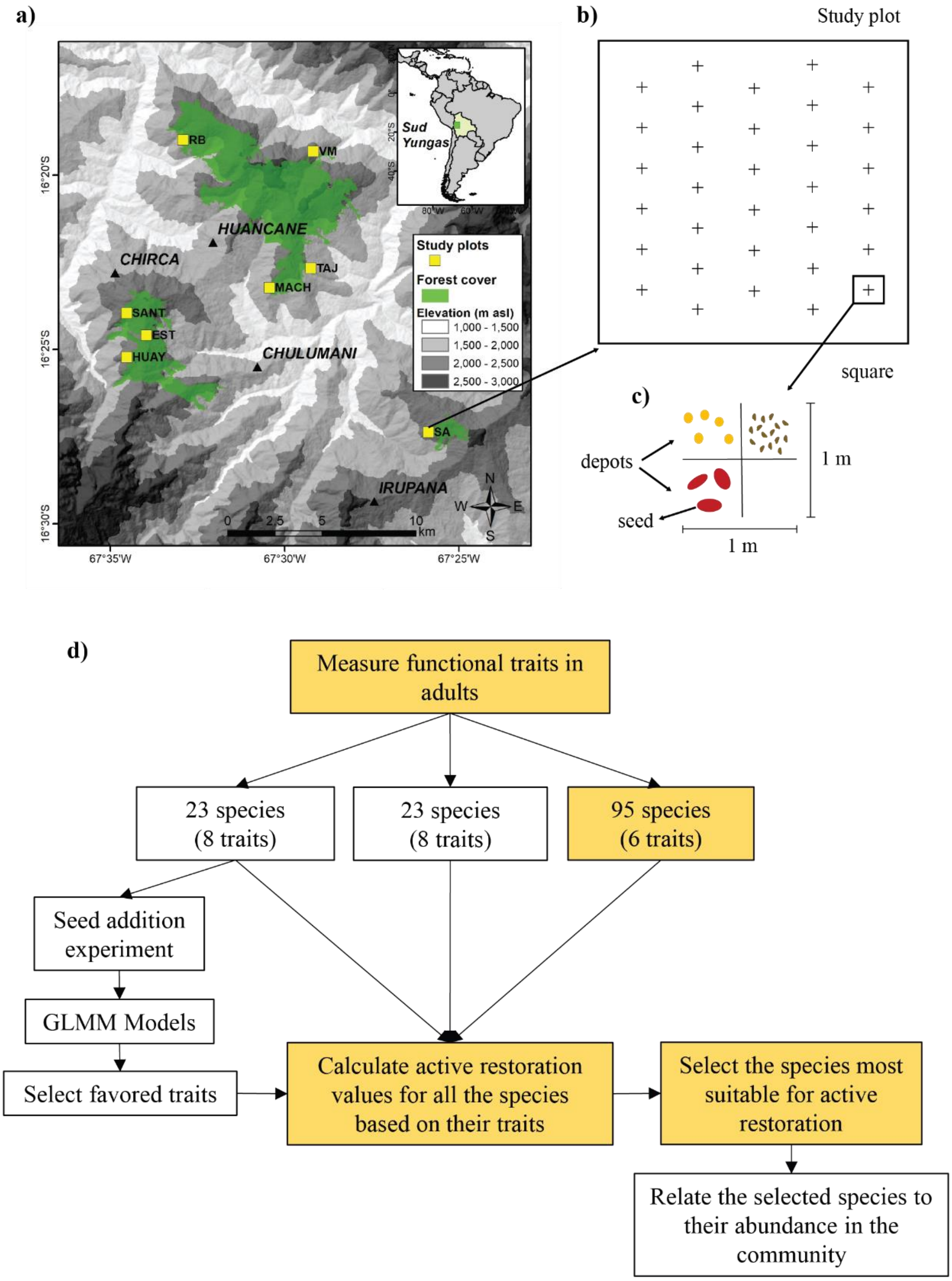


Figure S1. a) Study area showing the study plots; b) Setting of the experimental plots showing the arrangement of the squares; c) Detail of the squares (+), sub-squares and depots where seeds from different species (shown by different colors and sizes) were planted by direct seed addition; and d) Analytical framework, the yellow boxes show the procedure to be taken by stakeholders using the values in Table 1 or Figure 1.

Table S1. Species list, functional trait values for 46 species, and number of seeds planted per species in the direct seed addition experiment for 23 species (highlighted in bold). SS= Seed size (seed length, mm), SM= Seed mass (g), Disp= Dispersal vector.

Species	LA	SLA	LDMC	Bark	SSD	H_{max}	SS	SM	Disp	Planted seeds
Aiouea montana	49.6	111.4	428	3.5	0.55	16	11.1	0.22168	birds	96
Alchornea brittonii	138.2	70.2	442	3.2	0.55	14	5.6	0.03580	birds	320
Alchornea triplinervia* var. *crassifolia	42.6	79.6	483.5	5.1	0.62	11.5	3.7	0.03014	birds	320
Beilshmiedia latifolia	54.2	86.7	389	2.7	0.64	16	31.5	7.36350	birds	0
Beilshmiedia tovarensis	74.5	83.5	399.7	3.2	0.59	16	29.2	6.16500	birds	0
Brunellia rhoides	55.9	48.8	455.1	3.3	0.69	16	2.3	0.00205	wind	0
Cecropia elongata	3468.2	98.8	316.4	3.1	0.38	16.5	1.8	0.00109	bats	0
Clethra revoluta	62.8	67.4	400.7	3.6	0.56	15.5	1.4	0.00001	wind	1600
Clethra scabra* var. *laevigata	71	78.9	446.3	3.2	0.63	10	1.4	0.00001	wind	1600
Clusia elongata	65.4	49.6	288	4.2	0.61	17.5	4.8	0.01294	birds	320
Clusia lechleri	75.9	39.2	300.3	4.4	0.67	15.5	5.1	0.01448	birds	320
***Clusia* sp. nov.**	142.8	38.6	273.8	5.1	0.58	15.5	5.7	0.01744	birds	320
Clusia trochiformis	46.4	46.3	350.5	3.9	0.62	9.5	6.1	0.02725	birds	320
Coussapoa david-smithii	95.8	42.9	410	5.1	0.61	23.5	2.3	0.00185	birds	0
Ficus crassiuscula	23.3	57.5	424.8	4.7	0.63	23.5	1.8	0.00144	bats	0
Ficus cuatrecasasiana	109.9	98.5	344.7	3.1	0.53	17	1.2	0.00018	bats	640
Ficus maxima	99.9	127.9	302	2.7	0.43	14.5	2.3	0.00142	bats	640
Frangula sphaerosperma	50.5	164.9	393.8	2.5	0.57	9.5	5.4	0.02238	birds	320
Hedyosmum angustifolium	28.9	189.6	239.7	3.1	0.41	10.5	3.7	0.00696	birds	320
Hedyosmum racemosum	54.6	94.6	234.2	2.3	0.45	8	2.8	0.00347	birds	480
Hieronyma fendleri	23.2	57.7	376	4.7	0.61	8.3	4.6	0.02413	birds	0
Hieronyma sp. nov.	69.5	100.5	291.3	3.4	0.61	9	4.8	0.02853	birds	0
Hyptidendron arboreum	51.6	104.6	279.2	5.3	0.43	15.5	2.4	0.00041	wind	0
Inga adenophylla	26	53.7	467.6	3.6	0.78	14	8.4	0.10075	birds	0
Juglans boliviana	36.3	67.4	403.6	3.9	0.6	19.5	32.8	23.57740	auto	0
Mauria heterophylla	21.8	72.9	484.3	1.8	0.67	5.3	8	0.02790	birds	0
Miconia hygrophila	75.6	52.8	366.1	2.6	0.68	4.5	0.8		birds	0
Morella pubescens	10.8	91	479.7	3.5	0.7	9	3.1	0.01232	birds	0
Myrsine coriacea	19.8	84.2	429.4	3.2	0.73	10	3.3	0.02125	birds	0
Myrcia splendens	10	84.9	482.6	2.8	0.84	5	5.1	0.06321	birds	160
Ocotea puberula	49.8	131.6	468.2	4.2	0.64	9.3	7.7	0.21520	birds	0
Palicourea reticulata	83.3	198.6	320.4	2	0.53	5	3.9	0.01283	birds	320
Panopsis pearcei	26.4	65.3	393.8	3.2	0.65	7	30.1	13.05606	auto	0
Piper bolivianum	507.9	122.6	231.3	2.2	0.38	7.8	2.6	0.00365	bats	640
Piper elongatum	41.1	100.2	293.2	2.7	0.62	8.8	0.9	0.00022	bats	960
Podocarpus ingensis	2.4	48.7	511.8	9.9	0.75	15.5	7.7	0.02450	birds	0
Saurauia peruviana	96.2	141.5	309.7	3.9	0.41	11	1.1	0.00022	birds	0
Symplocos arechea	51.3	127.4	357.7	2.6	0.64	13	15.3	0.68593	birds	96

Vernonanthura patens	54	151.8	307.8	3.4	0.57	15.3	2.5	0.00043	wind	0
Viburnum seemenii	32	126	390	1.8	0.6	6	6.6	0.06893	birds	0
Vismia crassa	30.5	56.3	473.4	3.4	0.72	10.5	1.8	0.00045	bats	480
Vismia glaziovii	41.7	60.6	453.2	3.4	0.73	7.5	1.9	0.00052	bats	480
Vismia plicatifolia	30.3	118.9	385.8	1.9	0.63	6	2.5	0.00175	bats	0
Vismia cf. *rusbyi*	46	101	349.6	2.8	0.61	14.3	2	0.00084	bats	0
Weinmannia lechleriana	10.1	80.3	362.1	3.3	0.65	12	1	0.00010	wind	1600
Weinmannia sorbifolia	8.8	58.6	468.2	2.9	0.76	7	0.7	0.00008	wind	1600

Table S2. Example of the calculations to obtain the active restoration values for four species. RIT%: Relative importance of each trait %.

Traits	LA	SLA	LDMC	BarkT	SSD	SS	Hmax	Dispersal agent
Alc_bri	138.2	70.25	442.0	3.23	0.55	5.60	14.00	birds
Alc_tri	42.6	79.60	483.5	5.09	0.62	3.74	11.50	birds
Ver_pat	54.0	151.84	307.8	3.39	0.57	2.49	15.25	wind
Clu_tro	46.4	46.26	350.5	3.90	0.62	6.12	9.50	birds

Seed germination

Trait	SLA	LDMC	Hmax	BarkT	SS	DISP	Threshold:	GERM
Favored traits	<78	<357	<10.5	>3.25	>3	birds	0.25	R2=0.65
RIT%	4.74	12.03	2.31	7.52	39.14	34.26	Sum	Sum*R2
Alc_bri	4.74				39.14	34.26	78.14	50.788
Alc_tri				7.52	39.14	34.26	80.92	52.596
Ver_pat		12.03		7.52			19.56	12.713
Clu_tro	4.74	12.03	2.31	7.52	39.14	34.26	100	65

Seedling survival

Trait	HM	SS	DISP	Threshold:	SUR
Favored traits	<11.3	>3.6	All	0.5	R2=0.5
RIT%	34.14	26.36	39.5	Sum	Sum*R2
Alc_bri		26.36	39.5	65.86	32.93
Alc_tri		26.36	39.5	65.86	32.93
Ver_pat			39.5	39.5	19.75
Clu_tro	34.14	26.36	39.5	100	50

Seedling growth

Trait	LA	LDMC	SSD	SS	DISP	Threshold:	RGR
Favored traits	>47	<359	>0.57	<5.3	birds & wind	0.4	R2=0.38
RIT%	5.34	16.25	12.53	23.3	42.58	Sum	Sum*R2
Alc_bri	5.34				42.58	47.92	18.21
Alc_tri			12.53	23.3	42.58	78.41	29.796
Ver_pat	5.34	16.25		23.3	42.58	87.47	33.239
Clu_tro		16.25	12.53		42.58	71.36	27.117

Species	Active restoration value GERM+SUR+RGR	Active restoration value %
Alc_bri	101.93	**66.6**
Alc_tri	115.32	**75.4**
Ver_pat	65.70	**42.9**
Clu_tro	142.12	**92.9**

Table S3. Best generalized linear mixed-effect models, selected considering the best model with ΔAICc<2, in comparison to null models for a) seed germination, b) seedling survival, and c) relative growth rate (RGR).

Response variable	Variables included in the best models	df	AICc	ΔAICc	R2m
a) Germination	Bark thickness + (Bark thickness)^2 + Hmax + Seed size + LDMC + (LDMC)^2 + SLA + Disperser	12	762.4	0	0.65
	Null	3	970.6	208.2	0
b) Survival	Hmax + Seed size + Disperser	6	430.5	0	0.5
	Null	2	511.1	80.6	0
c) RGR	LA + Seed size + LDMC + SSD + Disperser	9	-82.3	0	0.38
	Null	3	-45.4	36.8	0

Table S4. Coefficients of the best generalized linear mixed-effect models with ΔAICc<2 for a) seed germination, b) seedling survival, and c) relative growth rate (RGR). For dispersal vector (Disp.) bat-dispersed species are in the intercept.

Response variable	Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)	
a) Germination	(Intercept)	-2.97	0.34	-8.64	<0.001	***
	SLA	-0.24	0.10	-2.45	0.014	*
	LDMC	-0.58	0.10	-5.74	<0.001	***
	LDMC^2	-0.20	0.10	-2.01	0.044	*
	Hmax	-0.62	0.14	-4.48	<0.001	***
	BarkT	0.52	0.15	3.39	<0.001	***
	BarkT^2	-0.24	0.07	-3.58	<0.001	***
	Seed size	1.26	0.20	6.19	<0.001	***
	Disp. Birds	1.44	0.41	3.52	<0.001	***
	Disp. Wind	0.67	0.43	1.56	0.118	
b) Survival	(Intercept)	-0.67	0.47	-1.42	0.155	
	Hmax	-0.63	0.09	-7.09	<0.001	***
	Seed size	1.32	0.20	6.73	<0.001	***
	Disp. Birds	0.02	0.46	0.05	0.958	

	Disp. Wind	3.24	0.61	5.31	<0.001	***
c) RGR	(Intercept)	0.19	0.07	2.85	0.004	**
	Disp. Birds	0.19	0.08	2.52	0.012	*
	Disp. Wind	0.38	0.08	4.83	<0.001	***
	LA	0.06	0.02	2.69	0.007	**
	Seed size	-0.07	0.03	-2.17	0.030	*
	LDMC	-0.07	0.02	-3.58	<0.001	***
	SSD	0.08	0.02	4.15	<0.001	***

Table S5. Partial and final active restoration values for 46 tree species with eight functional traits, showing their probabilities to surpass the filters in bracken-dominated areas. The R^2m values for these models were 0.65, 0.50 and 0.38 for seed germination, seedling survival and growth, respectively.

Abbrev.	Species	Germination	Survival	RGR	Active restoration value	Active restoration value (%)
Hie_spn	*Hieronyma* sp. nov.	61.9	50.0	38.0	149.9	98.0
Clu_tro	*Clusia trochiformis*	65.0	50.0	27.1	142.1	92.9
Pal_ret	*Palicourea reticulata*	57.0	50.0	33.2	140.3	91.7
Hed_ang	*Hedyosmum angustifolium*	57.0	50.0	31.2	138.2	90.4
Hie_fen	*Hieronyma fendleri*	57.2	50.0	29.8	137.0	89.5
Clu_elo	*Clusia elongata*	63.5	32.9	38.0	134.4	87.9
Clu_lec	*Clusia lechleri*	63.5	32.9	38.0	134.4	87.9
Myr_spl	*Myrcia splendens*	49.2	50.0	29.8	129.0	84.3
Oco_pub	*Ocotea puberula*	54.1	50.0	23.0	127.1	83.1
Clu_spn	*Clusia* sp. nov	63.5	32.9	29.1	125.6	82.1
Mau_het	*Mauria heterophylla*	52.3	50.0	20.9	123.2	80.5
Rha_sph	*Frangula sphaerosperma*	49.2	50.0	23.0	122.2	79.9
Mor_pub	*Morella pubescens*	54.1	36.8	29.8	120.7	78.9
Vib_spp	*Viburnum seemenii*	49.2	50.0	20.9	120.1	78.5
Myr_cor	*Myrsine coriacea*	49.2	36.8	29.8	115.8	75.7
Alc_tri	*Alchornea triplinervia* var. *boliviana*	52.6	32.9	29.8	115.3	75.4
Sym_are	*Symplocos arechea*	47.7	32.9	29.1	109.8	71.8
Ing_ade	*Inga adenophylla*	55.7	32.9	20.9	109.5	71.6
Pod_ing	*Podocarpus ingensis*	55.7	32.9	20.9	109.5	71.6
Sau_per	*Saurauia peruviana*	35.0	36.8	33.2	105.0	68.7
Aio_mon	*Aiouea montana*	52.6	32.9	18.2	103.7	67.8
Bei_lat	*Beilshmiedia latifolia*	47.7	32.9	23.0	103.6	67.7
Bei_tov	*Beilshmiedia tovarensis*	47.7	32.9	23.0	103.6	67.7
Alc_bri	*Alchornea brittonii*	50.8	32.9	18.2	101.9	66.6
Hed_rac	*Hedyosmum racemosum*	31.6	36.8	33.2	101.6	66.4
Mic_hyg	*Miconia hygrophila*	26.8	36.8	31.8	95.5	62.4
Pan_pea	*Panopsis pearcei*	30.0	50.0	4.8	84.8	55.4
Cou_dav	*Coussapoa david-smithii*	30.2	19.8	31.8	81.8	53.5

Wei_sor	*Weinmannia sorbifolia*	4.6	36.8	29.8	71.2	46.5
Jug_bol	*Juglans boliviana*	33.4	32.9	4.8	71.1	46.5
Cle_sca	*Clethra scabra* var. *laevigata*	1.5	36.8	31.8	70.1	45.8
Pip_elo	*Piper elongatum*	9.3	36.8	19.8	65.9	43.1
Hyp_arb	*Hyptidendron arboreum*	12.7	19.8	33.2	65.7	42.9
Ver_pat	*Vernonanthura patens*	12.7	19.8	33.2	65.7	42.9
Pip_bol	*Piper bolivianum*	9.3	36.8	17.1	63.2	41.3
Vis_cra	*Vismia crassa*	9.5	36.8	13.6	59.9	39.2
Vis_gla	*Vismia glaziovii*	9.5	36.8	13.6	59.9	39.2
Bru_rho	*Brunellia rhoides*	8.0	19.8	31.8	59.5	38.9
Cle_rev	*Clethra revoluta*	8.0	19.8	27.1	54.8	35.8
Wei_lec	*Weinmannia lechleriana*	4.9	19.8	29.8	54.4	35.6
Vis_pli	*Vismia plicatifolia*	1.5	36.8	13.6	51.9	33.9
Vis_rus	*Vismia* cf. *rusbyi*	7.8	19.8	19.8	47.4	31.0
Cec_elo	*Cecropia elongata*	7.8	19.8	17.1	44.6	29.2
Fic_cua	*Ficus cuatrecasasiana*	7.8	19.8	17.1	44.6	29.2
Fic_max	*Ficus maxima*	7.8	19.8	17.1	44.6	29.2
Fic_cra	*Ficus crassiuscula*	8.0	19.8	13.6	41.3	27.0

Table S6. Partial and final active restoration values of 95 tree and shrub species with six functional traits available from ten 20x20 m permanent plots (Missouri Botanical Garden – Bolivia Program 2024), showing their probabilities to surpass the filters in bracken-dominated areas. The R^2m values for these models were 0.65, 0.50 and 0.38 for seed germination, seedling survival and growth, respectively.

Family	Species	Germination	Survival	RGR	Active restoration value	Active restoration value (%)
Primulaceae	*Geissanthus ambigua*	52.3	50.0	31.8	134.1	87.7
Clusiaceae	*Clusia trochiformis*	52.3	50.0	29.8	132.1	86.3
Lauraceae	*Persea bilocularis*	52.3	50.0	29.8	132.1	86.3
Phyllanthaceae	*Hieronyma fendleri*	49.2	50.0	31.8	131.0	85.6
Primulaceae	*Myrsine latifolia*	49.2	50.0	31.8	131.0	85.6
Rosaceae	*Prunus guanaiensis*	49.2	50.0	31.8	131.0	85.6
Rosaceae	*Prunus pleiantha*	49.2	50.0	31.8	131.0	85.6
Rubiaceae	*Coussarea rudgeoides*	49.2	50.0	31.8	131.0	85.6
Rubiaceae	*Palicourea flavifolia*	49.2	50.0	31.8	131.0	85.6
Rubiaceae	*Palicourea tristis*	49.2	50.0	31.8	131.0	85.6
Cordiaceae	*Varronia cylindristachya*	49.2	50.0	29.8	129.0	84.3
Euphorbiaceae	*Alchornea triplinervia* var. *boliviana*	49.2	50.0	29.8	129.0	84.3
Monimiaceae	*Mollinedia lanceolata*	49.2	50.0	29.8	129.0	84.3
Myricaceae	*Morella pubescens*	49.2	50.0	29.8	129.0	84.3
Myrtaceae	*Myrcia* sp.	49.2	50.0	29.8	129.0	84.3
Myrtaceae	*Myrcia splendens*	49.2	50.0	29.8	129.0	84.3
Phyllanthaceae	*Hieronyma* sp. nov.	49.2	50.0	29.8	129.0	84.3

Primulaceae	*Myrsine coriacea*	49.2	50.0	29.8	129.0	84.3
Rhamnaceae	*Frangula sphaerocarpa*	49.2	50.0	29.8	129.0	84.3
Rosaceae	*Prunus pearcei*	49.2	50.0	29.8	129.0	84.3
Rubiaceae	*Randia micracantha*	49.2	50.0	29.8	129.0	84.3
Sapindaceae	*Allophylus cinnamomeus*	49.2	50.0	29.8	129.0	84.3
Chloranthaceae	*Hedyosmum racemosum*	49.2	50.0	27.1	126.3	82.5
Rubiaceae	*Palicourea reticulata*	49.2	50.0	27.1	126.3	82.5
Chloranthaceae	*Hedyosmum angustifolium*	49.2	50.0	25.0	124.2	81.2
Rubiaceae	*Palicourea attenuata*	49.2	50.0	25.0	124.2	81.2
Lauraceae	*Persea caerulea*	49.2	50.0	23.0	122.2	79.9
Sapindaceae	*Allophylus paniculatus*	49.2	50.0	23.0	122.2	79.9
Siparunaceae	*Siparuna grandiflora*	49.2	50.0	23.0	122.2	79.9
Anacardiaceae	*Mauria heterophylla*	49.2	50.0	20.9	120.1	78.5
Fabaceae	*Inga adenophylla*	49.2	50.0	20.9	120.1	78.5
Fabaceae	*Inga fendleriana*	49.2	50.0	20.9	120.1	78.5
Lauraceae	*Aiouea montana*	49.2	50.0	20.9	120.1	78.5
Myrtaceae	*Myrcia fenzliana*	49.2	50.0	20.9	120.1	78.5
Viburnaceae	*Viburnum seemenii*	49.2	50.0	20.9	120.1	78.5
Siparunaceae	*Siparuna tomentosa*	49.2	50.0	18.2	117.4	76.7
Clusiaceae	*Clusia elongata*	50.8	32.9	31.8	115.5	75.5
Styracaceae	*Styrax pentlandianus*	49.2	50.0	16.2	115.4	75.4
Clusiaceae	*Clusia ducu*	50.8	32.9	29.8	113.5	74.2
Euphorbiaceae	*Alchornea triplinervia* var. *crassifolia*	47.7	32.9	31.8	112.5	73.5
Monimiaceae	*Mollinedia repanda*	47.7	32.9	31.8	112.5	73.5
Myrtaceae	*Myrcia mollis*	47.7	32.9	31.8	112.5	73.5
Annonaceae	*Guatteria oblongifolia*	47.7	32.9	27.1	107.7	70.4
Celastraceae	*Zinowiewia australis*	26.9	50.0	29.8	106.7	69.8
Lauraceae	*Nectandra acutifolia*	50.8	32.9	23.0	106.7	69.7
Lauraceae	*Nectandra cuspidata*	50.8	32.9	20.9	104.7	68.4
Euphorbiaceae	*Alchornea brittonii*	47.7	32.9	23.0	103.6	67.7
Lauraceae	*Beilschmiedia latifolia*	47.7	32.9	23.0	103.6	67.7
Symplocaceae	*Symplocos colorata*	47.7	32.9	23.0	103.6	67.7
Ericaceae	*Cavendishia pubescens*	26.8	36.8	31.8	95.5	62.4
Melastomataceae	*Miconia hygrophila*	26.8	36.8	31.8	95.5	62.4
Fabaceae	*Collaea speciosa*	30.0	50.0	13.6	93.6	61.2
Aquifoliaceae	*Ilex hippocrateoides*	26.8	36.8	29.8	93.5	61.1
Ericaceae	*Gaultheria eriophylla*	26.8	36.8	29.8	93.5	61.1
Actinidiaceae	*Saurauia peruviana*	23.8	36.8	31.8	92.4	60.4
Melastomataceae	*Miconia brittonii*	23.8	36.8	31.8	92.4	60.4
Melastomataceae	*Miconia cordata*	23.8	36.8	31.8	92.4	60.4
Pentaphylacaceae	*Freziera lanata*	25.4	36.8	29.8	92.0	60.1
Lythraceae	*Adenaria floribunda*	23.8	36.8	29.8	90.4	59.1
Melastomataceae	*Miconia cyanocarpa* var. *hirsuta*	23.8	36.8	29.8	90.4	59.1
Melastomataceae	*Miconia elongata*	23.8	36.8	29.8	90.4	59.1

Melastomataceae	*Miconia minutiflora*	23.8	36.8	25.0	85.6	56.0
Proteaceae	*Panopsis pearcei*	26.9	50.0	4.8	81.7	53.4
Brunelliaceae	*Brunellia rhoides*	25.4	19.8	31.8	76.9	50.3
Clethraceae	*Clethra cuneata*	4.6	36.8	29.8	71.2	46.5
Clethraceae	*Clethra revoluta*	4.6	36.8	29.8	71.2	46.5
Cunoniaceae	*Weinmannia sorbifolia*	4.6	36.8	29.8	71.2	46.5
Rubiaceae	*Bathysa australis*	1.5	36.8	31.8	70.1	45.8
Rubiaceae	*Chimarrhis* sp.	1.5	36.8	31.8	70.1	45.8
Rubiaceae	*Ladenbergia oblongifolia*	1.5	36.8	31.8	70.1	45.8
Cannabaceae	*Trema micrantha*	22.3	19.8	27.1	69.1	45.2
Asteraceae	*Kaunia longipetiolata*	1.5	36.8	29.8	68.1	44.5
Cunoniaceae	*Weinmannia rhoifolia*	1.5	36.8	29.8	68.1	44.5
Ericaceae	*Bejaria aestuans*	1.5	36.8	29.8	68.1	44.5
Escalloniaceae	*Escallonia paniculata*	1.5	36.8	29.8	68.1	44.5
Melastomataceae	*Pleroma stenocarpum*	1.5	36.8	29.8	68.1	44.5
Asteraceae	*Lepidaploa beckii*	1.5	36.8	27.1	65.4	42.7
Asteraceae	*Baccharis brachylaenoides*	1.5	36.8	25.0	63.4	41.4
Asteraceae	*Baccharis latifolia*	1.5	36.8	25.0	63.4	41.4
Asteraceae	*Baccharis nitida*	1.5	36.8	25.0	63.4	41.4
Asteraceae	*Oyedaea boliviana*	1.5	36.8	25.0	63.4	41.4
Asteraceae	*Raulinoreitzia crenulata*	1.5	36.8	25.0	63.4	41.4
Hypericaceae	*Vismia crassa*	4.6	36.8	13.6	55.0	36.0
Clethraceae	*Clethra scabra* var. *laevigata*	3.1	19.8	31.8	54.7	35.7
Piperaceae	*Piper crassinervium*	1.5	36.8	15.6	54.0	35.3
Piperaceae	*Piper elongatum*	1.5	36.8	15.6	54.0	35.3
Piperaceae	*Piper hispidum*	1.5	36.8	15.6	54.0	35.3
Piperaceae	*Piper trichorhachis*	1.5	36.8	15.6	54.0	35.3
Solanaceae	*Solanum actaeibotrys*	1.5	36.8	15.6	54.0	35.3
Solanaceae	*Solanum acuminatum*	1.5	36.8	15.6	54.0	35.3
Asteraceae	*Vernonanthura patens*	0.0	19.8	31.8	51.6	33.7
Melastomataceae	*Meriania brittoniana*	0.0	19.8	31.8	51.6	33.7
Solanaceae	*Solanum roseum*	1.5	36.8	10.9	49.2	32.2
Asteraceae	*Critoniopsis boliviana*	0.0	19.8	25.0	44.8	29.3
Urticaceae	*Cecropia elongata*	3.1	19.8	15.6	38.5	25.1

Supplementary material Chaper VI

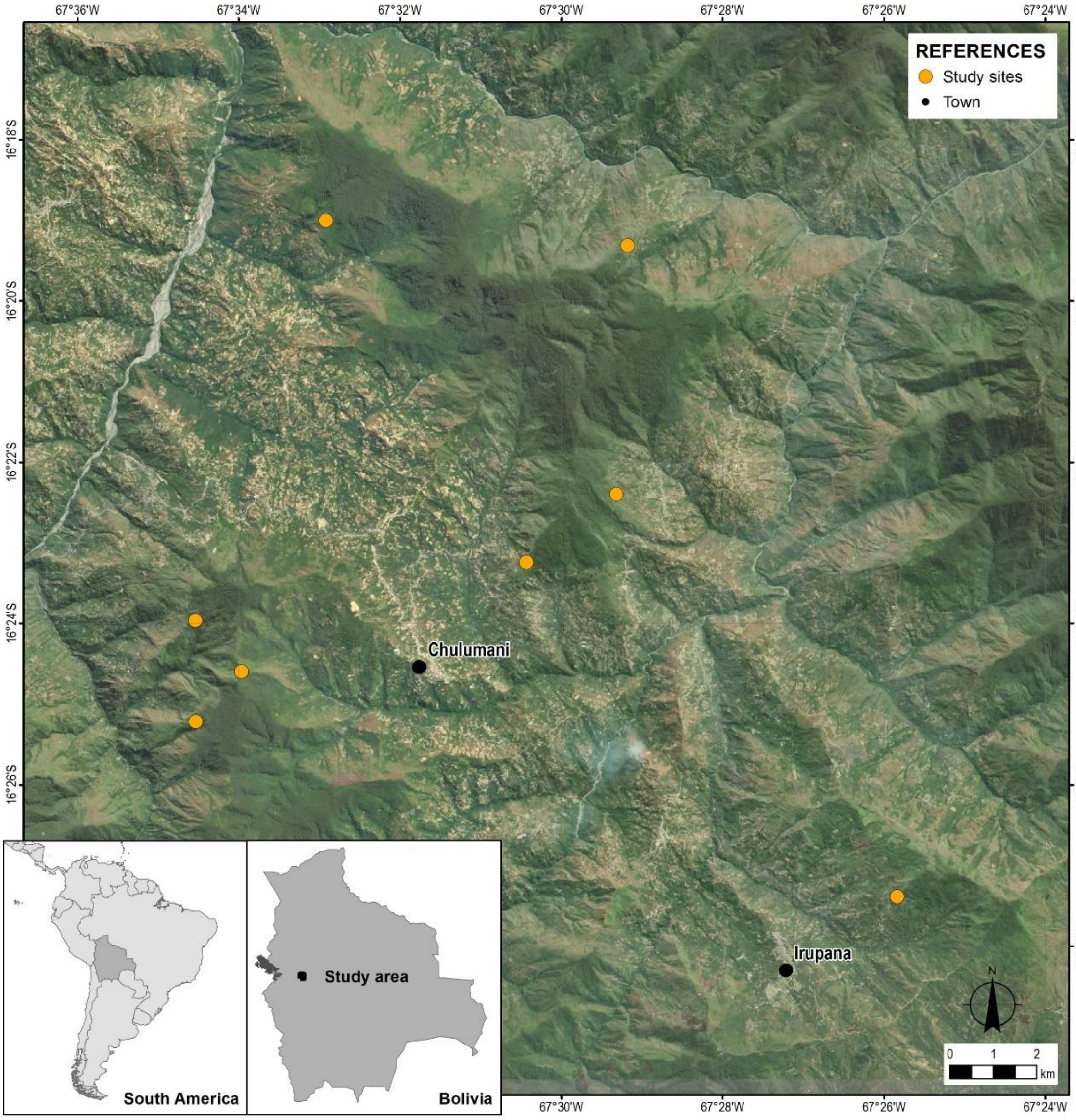


Fig. S1. Map of the study area in Sud Yungas, La Paz, Bolivia. The eight study sites were established at 100 m from the forest borders.

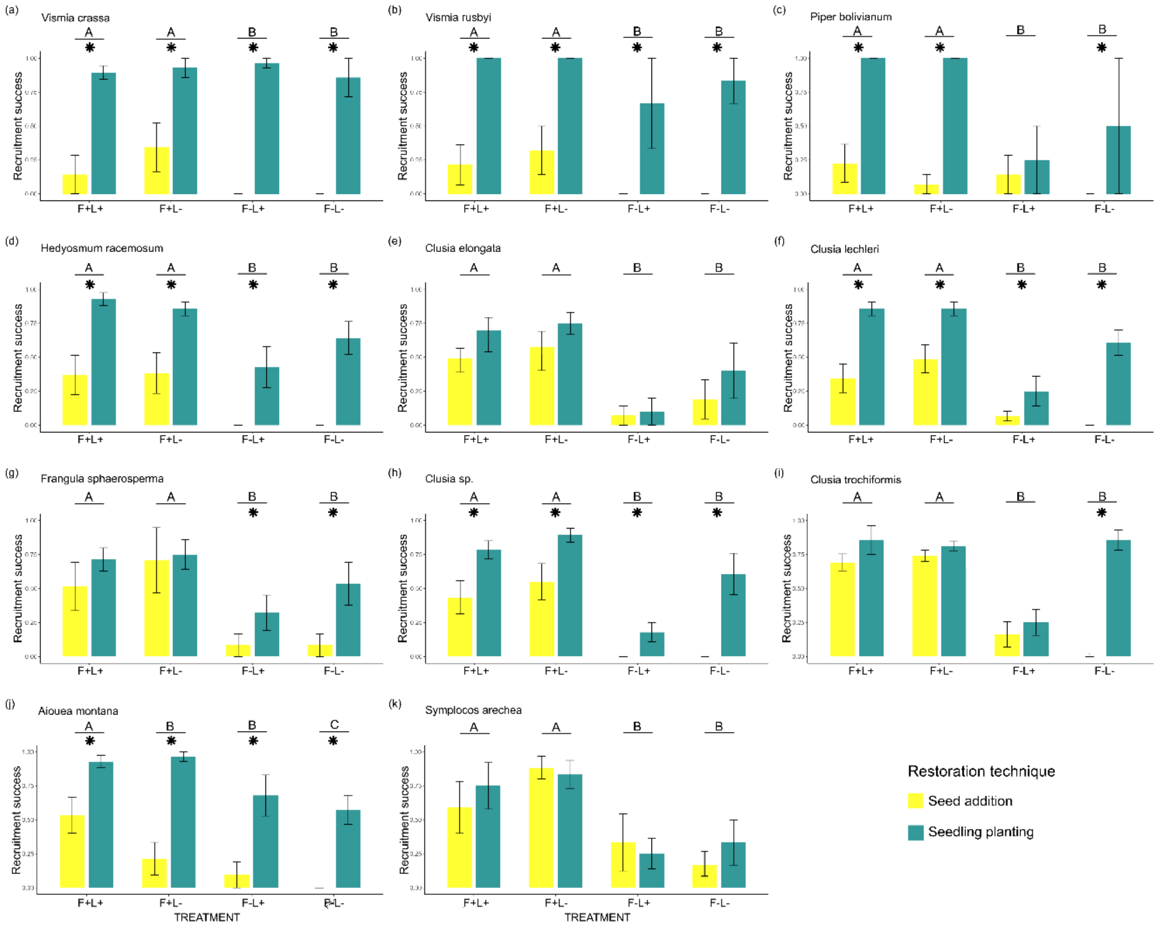


Fig. S2. Proportion of seedlings obtained in experimental bracken management treatments for each species by seed addition and seedling planting after three years. Treatments are labeled as follows: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots show the predicted values from the generalized linear mixed-effects models (GLMMs) ± SE. Capital letters indicate differences among treatments and asterisks indicate significant differences ($p < 0.05$) between restoration techniques.

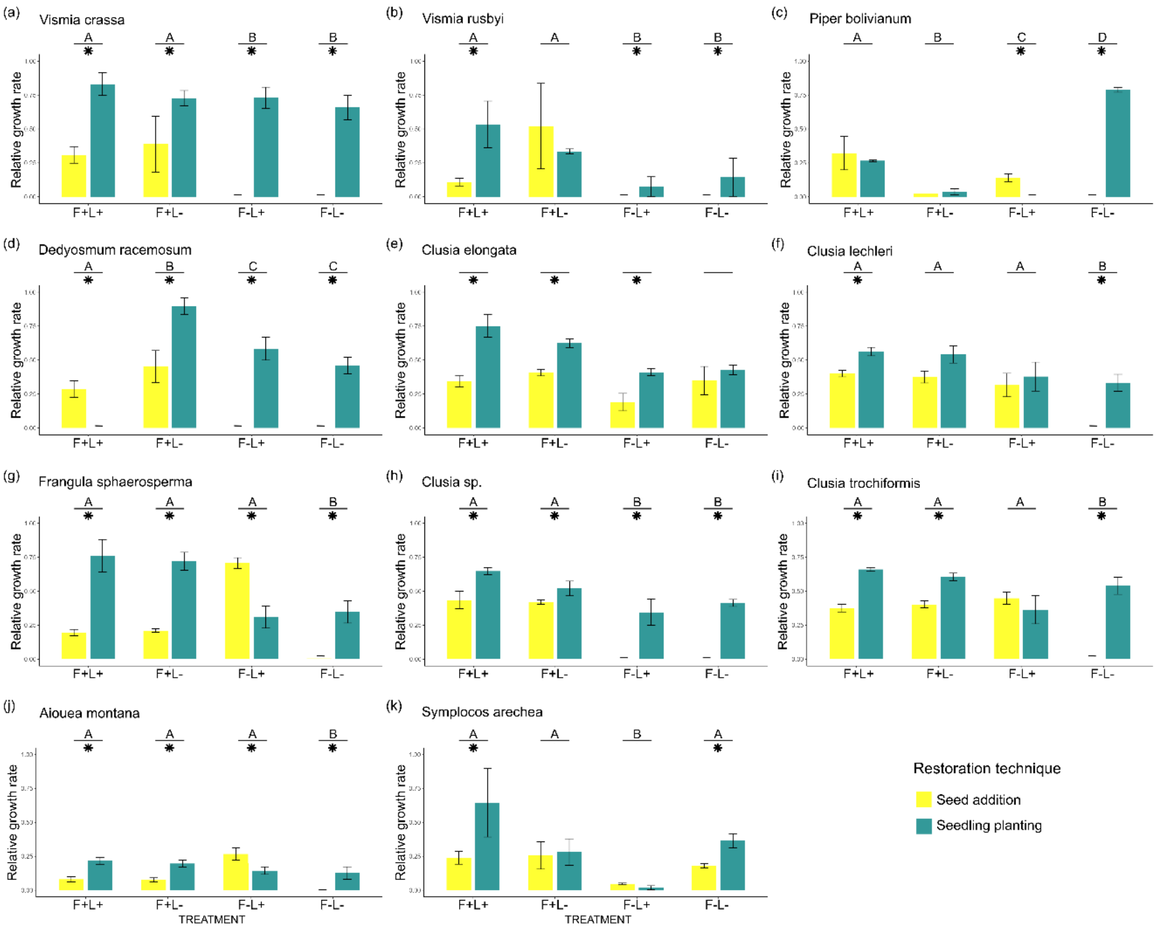


Fig. S3. Relative growth rate of seedlings in experimental bracken management treatments for each species by seed addition and seedling planting after three years. Treatments are labeled as follows: (F+) bracken fronds present, (F-) bracken fronds removed, (L+) bracken litter present, and (L-) bracken litter removed. The bar plots represent predicted values from the generalized linear mixed-effects models (GLMMs) ± SE. Capital letters indicate differences between treatments and asterisks indicate significant differences ($p < 0.05$) between restoration techniques.

Table S1. Generalized Generalized linear mixed effects models (GLMM) for recruitment success and Relative growth rate. Treatment with fronds and litter present (F+L+) and seed addition technique are in the intercept.

Recruitment success

	Estimate	Std. Error	z value	Pr(>|z|)	LRT test p-value	R2 marginal
(Intercept)	-0.02	0.15	-0.18	0.85	**<0.001**	0.63
F+L-	0.11	0.14	0.76	0.44		
F-L+	-1.84	0.24	-7.65	**<0.001**		
F-L-	-3.26	0.43	-7.46	**<0.001**		
Transplant	1.01	0.17	6.10	**<0.001**		
F+L-:Transplant	0.01	0.23	0.05	0.96		
F-L+:Transplant	0.55	0.29	1.90	**0.04**		
F-L-:Transplant	2.47	0.47	5.29	**<0.001**		

Relative growth rate

	Estimate	Std. Error	z value	Pr(>|z|)		
(Intercept)	2.04	0.14	14.46	**<0.001**	**<0.001**	0.74
F+L-	-0.06	0.19	-0.31	0.76		
F-L+	-1.53	0.29	-5.10	**<0.001**		
F-L-	-2.52	0.44	-5.68	**<0.001**		
Transplant	1.44	0.15	9.42	**<0.001**		
F+L-:Transplant	0.76	0.32	2.35	**0.02**		
F-L+:Transplant	0.01	0.22	0.05	0.95		
F-L-:Transplant	0.80	0.46	1.75	0.08		

Table S2. Generalized linear mixed effects models (GLMM) for recruitment success of each species. Treatment with fronds and litter present (F+L+) and seed addition technique are in the intercept.

Vismia crassa

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.38	0.86	-2.31	**0.02**
F+L-	2.97	1.46	2.03	0.06
F-L+	-5.83	1.04	-3.99	**<0.001**
F-L-	-5.83	1.06	-3.78	**<0.001**
Transplant	4.48	1.03	3.06	**0.002**
F+L-:Transplant	-4.07	1.56	-2.78	**0.005**
F-L+:Transplant	5.83	1.44	3.99	**<0.001**
F-L-:Transplant	5.84	1.98	2.94	**0.003**

Vismia rusbyi

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.98	0.88	-3.41	**<0.001**
F+L-	2.01	1.01	2.01	0.07
F-L+	-2.03	0.95	-2.98	**0.002**
F-L-	-2.14	0.97	-1.98	**0.003**
Transplant	4.39	1.29	3.39	**<0.001**
F+L-:Transplant	-1.89	1.35	-1.44	**0.03**
F-L+:Transplant	-0.85	1.83	-2.19	**0.02**
F-L-:Transplant	1.36	1.46	2.88	**0.003**

Piper bolivianum

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.98	0.88	-3.41	**<0.001**
F+L-	2.01	1.01	1.99	0.06
F-L+	-2.33	0.95	-3.51	**<0.001**
F-L-	-3.33	0.97	-3.62	**<0.001**
Transplant	4.39	1.29	3.39	**<0.001**
F+L-:Transplant	-3.33	0.58	-5.72	**<0.001**
F-L+:Transplant	-0.28	0.11	-1.78	0.35
F-L-:Transplant	2.47	0.77	3.22	**0.001**

Hedyosmum racemosum

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.05	0.36	-0.15	0.88
F+L-	0.11	0.47	0.23	0.82
F-L+	-3.67	0.83	-4.41	**<0.001**
F-L-	-3.67	0.83	-4.41	**<0.001**
Transplant	1.53	0.58	2.62	**0.01**
F+L-:Transplant	-1.95	0.71	-2.75	**0.005**
F-L+:Transplant	2.11	1.01	2.10	**0.03**
F-L-:Transplant	2.29	0.98	2.33	**0.02**

Clusia elongata

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.08	0.33	-0.24	0.81
F+L-	0.09	0.37	0.25	0.81
F-L+	-1.78	0.75	-2.36	**0.02**
F-L-	-1.33	0.71	-2.01	**0.04**
Transplant	0.66	0.44	1.50	0.13
F+L-:Transplant	0.29	0.61	0.48	0.63
F-L+:Transplant	-0.41	0.95	-0.43	0.67
F-L-:Transplant	0.77	0.92	0.84	0.4

Clusia lechleri

	stimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.50	0.33	-1.52	0.13
F+L-	0.45	0.37	1.23	0.22
F-L+	-1.38	0.54	-2.59	**<0.001**
F-L-	-3.45	0.83	-4.13	**<0.001**
Transplant	1.94	0.48	4.01	**<0.001**
F+L-:Transplant	1.28	0.29	4.44	**<0.001**
F-L+:Transplant	1.87	0.82	2.28	**0.02**
F-L-:Transplant	2.28	0.95	2.40	**0.02**

Frangula sphaerosperma

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.67	0.36	1.85	0.06
F+L-	0.19	0.61	0.31	0.76
F-L+	-2.20	0.56	-3.96	**<0.001**
F-L-	-2.20	0.56	-3.96	**<0.001**
Transplant	-0.16	0.38	-0.43	0.67
F+L-:Transplant	-0.39	0.69	-0.57	0.57
F-L+:Transplant	1.74	0.61	2.83	**0.005**
F-L-:Transplant	2.03	0.65	3.12	**0.002**

Clusia sp.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.18	0.29	-0.61	0.54
F+L-	0.50	0.38	1.32	0.19
F-L+	-3.98	0.91	-4.37	**<0.001**
F-L-	-3.69	0.83	-4.45	**<0.001**
Transplant	1.02	0.41	2.53	**0.01**
F+L-:Transplant	-0.24	0.66	-0.36	0.72
F-L+:Transplant	2.24	0.98	2.28	**0.02**
F-L-:Transplant	2.71	0.94	2.89	**0.003**

Clusia trochiformis

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.75	0.32	2.35	**0.02**
F+L-	0.29	0.31	0.93	0.35
F-L+	-1.98	0.42	-4.77	**<0.001**
F-L-	-4.84	0.83	-5.84	**<0.001**
Transplant	0.22	0.47	0.47	0.64
F+L-:Transplant	1.08	0.91	1.18	0.24
F-L+:Transplant	0.21	0.62	0.33	0.74
F-L-:Transplant	5.11	1.01	5.04	**<0.001**

Aiouea montana

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.44	0.38	1.15	0.25
F+L-	-0.92	0.44	-1.08	**0.03**
F-L+	-1.93	0.65	-2.98	**0.002**
F-L-	-4.57	0.87	-5.27	**<0.001**
Transplant	1.14	0.54	2.12	**0.03**
F+L-:Transplant	1.28	0.29	4.44	**<0.001**
F-L+:Transplant	0.76	0.20	3.74	**<0.001**
F-L-:Transplant	2.98	1.01	2.94	**0.003**

Symploccos arechea

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.99	0.29	5.00	**<0.001**
F+L-	0.77	0.68	1.12	0.78
F-L+	-2.42	0.97	-2.00	**0.01**
F-L-	-10.31	1.51	-6.82	**<0.001**
Transplant	-1.39	0.58	-2.37	**<0.001**
F+L-:Transplant	-0.89	0.83	0.94	0.87
F-L+:Transplant	2.42	0.97	2.00	**0.01**
F-L-:Transplant	10.60	1.51	7.02	**<0.001**

Table S3. Generalized linear mixed effects models (GLMM) for relative growth rate of each specie. Treatment with fronds and litter present (F+L+) and seed addition technique are in the intercept.

Vismia crassa

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.15	0.10	1.48	0.14
F+L-	0.23	0.14	1.70	0.09
F-L+	-1.25	0.37	-3.36	**<0.001**
F-L-	-1.32	0.38	-3.47	**<0.001**
Transplant	0.68	0.11	5.94	**<0.001**
F+L-:Transplant	-0.41	0.16	-2.54	**0.01**
F-L+:Transplant	2.37	0.69	3.41	**<0.001**
F-L-:Transplant	-1.51	0.70	-2.15	**0.03**

Vismia rusbyi

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.22	0.16	1.39	0.16
F+L-	0.15	0.13	1.18	0.24
F-L+	-1.48	0.71	-2.10	**0.03**
F-L-	-1.44	0.71	-2.98	**0.02**
Transplant	0.45	0.11	4.01	**<0.001**

F+L-:Transplant	-0.46	0.80	-0.51	0.56
F-L+:Transplant	-0.37	0.16	-2.35	**0.01**
F-L-:Transplant	-0.30	0.15	-2.03	**0.04**

Piper bolivianum

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.24	0.07	3.46	**0.001**
F+L-	-1.23	0.42	-2.94	**0.003**
F-L+	-0.16	0.04	-3.70	**<0.001**
F-L-	-0.15	0.07	-2.12	**0.034**
Transplant	-0.01	0.09	-0.06	0.95
F+L-:Transplant	-0.13	0.07	-1.77	0.08
F-L+:Transplant	0.90	0.11	8.55	**<0.001**
F-L-:Transplant	0.65	0.09	7.47	**<0.001**

Hedyosmum racemosum

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.28	0.09	3.09	**0.002**
F+L-	2.95	0.38	7.76	**<0.001**
F-L+	-0.27	0.13	-2.10	**0.03**
F-L-	-0.27	0.13	-2.12	**0.03**
Transplant	0.82	0.11	7.50	**<0.001**
F+L-:Transplant	-0.36	0.15	-2.36	**0.02**
F-L+:Transplant	-1.74	0.38	-4.52	**<0.001**
F-L-:Transplant	-0.37	0.16	-2.37	**0.01**

Clusia elongata

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.34	0.04	9.48	**<0.001**
F+L-	0.06	0.04	1.50	0.13
F-L+	-0.08	0.09	-0.89	0.37
F-L-	0.04	0.07	0.64	0.52
Transplant	0.40	0.05	8.48	**<0.001**
F+L-:Transplant	-0.19	0.07	-2.89	**0.003**
F-L+:Transplant	-0.25	0.12	-2.03	**0.03**
F-L-:Transplant	-0.38	0.09	-4.11	**<0.001**

Clusia lechleri

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.40	0.05	8.17	**<0.001**
F+L-	-0.02	0.07	-0.37	0.71

F-L+	-0.08	0.08	-0.99	0.32
F-L-	-0.40	0.08	-5.17	**<0.001**
Transplant	0.16	0.07	2.44	**0.01**
F+L-:Transplant	0.00	0.09	0.03	0.97
F-L+:Transplant	-0.10	0.11	-0.88	0.38
F-L-:Transplant	-1.23	0.42	-2.94	**0.003**
Frangula sphaerosperma				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.20	0.09	2.11	**0.03**
F+L-	0.02	0.07	0.22	0.83
F-L+	-0.13	0.10	-1.22	0.22
F-L-	0.57	0.10	5.52	**<0.001**
Transplant	0.57	0.06	8.96	**<0.001**
F+L-:Transplant	-2.05	0.56	-3.67	**0.002**
F-L+:Transplant	-1.12	0.12	-9.30	**<0.001**
F-L-:Transplant	-0.38	0.12	-3.27	**0.001**
Clusia sp.				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.43	0.04	11.02	**<0.001**
F+L-	-0.01	0.06	-0.26	0.79
F-L+	-0.43	0.06	-6.97	**<0.001**
F-L-	-0.43	0.06	-7.43	**<0.001**
Transplant	0.21	0.05	3.98	**<0.001**
F+L-:Transplant	-0.58	0.53	-2.02	**0.02**
F-L+:Transplant	-1.51	0.70	-2.15	**0.03**
F-L-:Transplant	0.20	0.08	2.51	**0.012**
Clusia trochiformis				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.38	0.04	9.67	**<0.001**
F+L-	0.03	0.05	0.55	0.58
F-L+	0.06	0.07	0.97	0.33
F-L-	-0.37	0.06	-6.24	**<0.001**
Transplant	0.29	0.05	5.68	**<0.001**
F+L-:Transplant	-0.08	0.07	-2.78	**0.001**
F-L+:Transplant	-0.06	0.04	-1.39	0.16
F-L-:Transplant	0.25	0.08	3.22	**0.001**
Aiouea montana				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.08	0.03	2.85	**0.004**

F+L-	0.01	0.04	0.33	0.74
F-L+	0.15	0.07	1.89	0.31
F-L-	-0.36	0.09	-4.19	**<0.001**
Transplant	0.14	0.03	4.14	**<0.001**
F+L-:Transplant	-0.03	0.05	-2.15	**0.001**
F-L+:Transplant	-0.22	0.07	-2.93	**0.003**
F-L-:Transplant	-0.03	0.05	-2.01	**0.001**
Symplocos arechea				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.24	0.13	1.80	0.07
F+L-	0.02	0.17	0.11	0.91
F-L+	-1.04	0.56	-3.65	**<0.001**
F-L-	-0.07	0.29	-0.23	0.82
Transplant	0.41	0.17	2.32	**0.02**
F+L-:Transplant	-0.38	0.23	-1.66	0.10
F-L+:Transplant	-0.44	0.36	-1.24	0.21
F-L-:Transplant	-0.21	0.36	-2.18	**0.002**

Vorlage

Bestätigung des Betreuers der Dissertation von Frau Cecilia Lorena López Alípaz

Hiermit bestätige ich als Betreuer/in der o. g. Dissertation, dass die gemeinsame Arbeit mehrerer Personen an der Arbeit durch den Forschungsgegenstand gerechtfertigt ist.

Mit freundlichen Grüßen,

Datum:

____

Prof. Dr. Isabell Hensen

Beiträge aller Autoren (Author contributions)

Chapter 2

López, C. L., Mayta, C., Fuentes, A. F., Villegas, M., Jiménez, E. A., Vasquez, V., Hensen, I., & Gallegos, S. C. (2024). Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-disturbed tropical montane habitats. *Forest Ecology and Management*, 566, 122056. DOI: 10.1016/j.foreco.2024.122056

	CL [75%]	CM [1%]	AF [1%]	MV [1%]	EJ [1%]	VV [1%]	IH [10%]	SG [10%]
Entwurf (Design)	30	0	0	0	0	0	35	35
Umsetzung (Implementation)	85	2	3	1	2	2	0	5
Auswertung (Analysis)	95	2	0	0	0	0	0	5
Schreiben (Writing)	90	0	0	0	0	0	5	5

Chapter 3

Jiménez, E. A., **López, C. L.,** Fuentes, A. F., Hensen, I., & Gallegos, S. C. Influence of Pteridium fronds and leaf litter management on the soil seed bank characteristics in a fire-disturbed tropical montane forest. (*under review* in *Biotropica* since *07.02.2025)*

	EJ [33%]	**CL [32%]**	AF [3%]	IH [11%]	SG [21%]
Entwurf (Design)	0	30	0	35	35
Umsetzung (Implementation)	10	55	10	0	25
Auswertung (Analysis)	60	30	0	0	10
Schreiben (Writing)	60	10	5	10	15

Chapter 4

López, C. L., Mayta, C., Soliz, C. A., Hensen, I., & Gallegos, S. C. (2025). Facilitative and competitive effects of bracken fronds and litter on tree seedling recruitment. *Frontiers in Ecology and Evolution.* DOI: 10.3389/fevo.2025.1534920

	CL [76%]	CM [5%]	AS [2%]	IH [8%]	SG [9%]
Entwurf (Design)	65	5	0	15	15
Umsetzung (Implementation)	80	5	5	5	5
Auswertung (Analysis)	80	5	0	5	10
Schreiben (Writing)	80	5	5	5	5

Chapter 5

Gallegos, S. C., **López, C. L.,** Naoki, K., Solíz, C.A., Fuentes, A. F., Mayta, C., Cayola, L., Tello, J. S., & Hensen, I. A trait-based approach for restoring tropical forest in fire-deforested bracken-dominated areas. (*under review* in *Journal of Applied Ecology since 17.12.2024)*

	SG [50%]	**CL [31%]**	KN [3%]	AS [1%]	AF [1%]	CM [2%]	LC [1%]	ST [1%]	IH [10%]
Entwurf (Design)	35	30	0	0	0	0	0	0	35
Umsetzung (Implementation)	47	47	0	2	2		1	1	0
Auswertung (Analysis)	50	35	10	0	0	5	0	0	0
Schreiben (Writing)	70	10	5	0	0	5	0	0	5

Chapter 6

López, C. L., Mayta, C., Hensen, I., & Gallegos, S. C. Comparison of seed addition and seedling planting for the restoration of bracken-dominated areas under different management methods

	CL [73%]	CM [5%]	IH [9%]	SG [13%]
Entwurf (Design)	35	5	30	30
Umsetzung (Implementation)	85	5	0	10
Auswertung (Analysis)	85	5	0	10
Schreiben (Writing)	85	5	5	5

Datum:

Cecilia López *Prof. Dr. Isabell Hensen*

C.V.

CECILIA LORENA LOPEZ ALIPAZ, M.Sc

Date of birth:
Place of birth:
Adress:
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EDUCATION

2019 - Present:	***PhD student*, **Institute of Geobotany and Botanical Garden, Martin-Luther University Halle Wittenberg (MLU). Halle (Saale), Germany. Thesis title: "The role of bracken's fronds and litter on tree seedling performance in a tropical montane forest: a trait based approach". Supervisors: Dr. Prof. Isabell Hensen (MLU) and Dr. Silvia C. Gallegos (MLU)
2018 - 2019:	***Master of Science in Biology,*** Department of Biology. Universidad Mayor de San Andrés. La Paz, Bolivia. Thesis title*: "Effect of the application of different sources of mycorrhizal inoculum".* Supervisors: Dr. Prof. Kazuya Naoki (UMSA) and Dr. Silvia C. Gallegos (MLU).
2011 - 2017:	***Bachelor in Biology,*** *Universidad Mayor de San Andrés (Department of Biology),* Thesis title *"Aspects of the floral and reproductive biology of the Queñua (Polylepis incarum*, Rosaceae*), in the community of Kopacati, La Paz-Bolivia".* Supervisors: Prof. Emilia García (UMSA), Dr. Alejandra Domic (UPenn) and Dr. Silvia Gallegos (MLU)

WORK EXPERIENCE

2017 – 2019:	Laboratory assistant in the Project "Climate change and anthropogenic impact effects on the distribution of *Polylepis* woodlands in the Andes of northern Chile during the last 15,000 years". CEAZA (Centro de análisis avanzado en zonas áridas – Chile)- LPB (Herbario Nacional de Bolivia).
2017	Research Assistant in the project "Evaluation of the effect of establishing a pilot dairy cattle barn as an adaptative management strategy to climate change, in the ayllu Corpa". Universidad Mayor de San Andrés - Instituto de Ecología. Scholarship job.
2016	Research Assistant. (LPB) Herbario Nacional de Bolivia.
2016	Teaching assistant for the course Botany 2 BOT-202, with 20 hrs / month. From August to December. Biology Department. Universidad Mayor de San Andrés.

2015	Teaching assistant for the course Botany 2 BOT-202, with 20 hrs / month. From August to December. Biology Department. Universidad Mayor de San Andrés.
2015	Laboratory Assistant in the Project “Germination of four species of *Polylepis* genus for reforestation seedlings production to urban green areas in the Municipality of La Paz and its revaluation as a native species”. Universidad Mayor de San Andrés - Instituto de biología molecular y biotecnología. Scholarship job.
2014	Fieldwork and Laboratory Assistant in the Project “Ecology and conservation of two endangered Andean trees species (*Polylepis incarum* and *Polylepis pacensis*, Rosaceae) in the department of La Paz. Asociación Sueca de Desarrollo Internacional – Universidad Mayor de San Andrés – Herbario Nacional de Bolivia.
2013	Database Assistant. Herbario Nacional de Bolivia.
2011-2012	Fieldwork and Laboratory Assistant. Colección Boliviana de Fauna, Herpetology Department.

ADDITIONAL INFORMATION

GRANTS

Grant #05-16	Name of Funding Organization: FOUNDATION FOR THE DEVELOPMENT OF ECOLOGY (FUNDECO) - UNIVERSIDAD MAYOR DE SAN ANDRÉS. Amount Awarded: $ 1200. Period of Grant Award: May 2016 – Sept 2017. Title of Project: “Phenological study of the Queñua (*Polylepis incarum*, Rosaceae in the community of Kopacati (Copacabana, La Paz - Bolivia)”. Role on Project: Main researcher
Grant #07	Name of Funding Organization: SUPPORT PROGRAM FOR THE SUSTAINABLE CONSERVATION OF BIODIVERSITY (PACsBIO) – EUROPEAN UNION. Amount Awarded: $ 1800. Period of Grant Award: June – December 2016. Title of Project: “Monitoring of the effects of the pathogenic fungus *Leptosphaeria polylepidis* in *Polylepis tarapacana* forests of the Sajama National Park”. Role on Project: Main researcher

Publications

López, C. L., Mayta, C., Fuentes, A. F., Villegas, M., Jiménez, E. A., Vasquez, V., Hensen, I. & Gallegos, S. C. (2024). Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-disturbed tropical montane habitats. *Forest Ecology and Management, 566, 122056.*

López, C. L., Mayta, C., Solíz, C. A., Hensen, I. & Gallegos, S. C. Facilitative and competitive effects of bracken fronds and litter on tree seedling recruitment. Accepted for publication in *Frontiers in Ecology and Evolution*

Beck, S. G., Fuentes, A. F., **López, C. L.,** Cuba-Orozco, E., & Gallegos, S. C. (2024). Los bosques montanos húmedos de la serranía de Apa-Apa (Sud Yungas, La Paz, Bolivia): Un centro de diversidad de plantas y fuente esencial de agua. *Ecologia En Bolivia*, 59(2), 85–151.

Villegas, M., Mayta, C., **López, C. L.,** Hensen, I. & Gallegos, S. C. (2024). Bird communities respond to the seasonal fruit and flower availability in a fragmented tropical andean landscape. *Ornitología tropical*, 35: 38-45.

Mayta, C., **López, C. L.,** Villegas, M., Aguirre, L. F., Hensen, I., & Gallegos, S. C. (2024). Bird perches and artificial bat roosts increase seed rain and seedling establishment in tropical bracken-dominated deforested areas. *Restoration Ecology*, e14197.

López, C. L., Mayta, C., Naoki, K., Quezada, J. A., Hensen, I., & Gallegos, S. C. (2022). Bracken fern does not diminish arbuscular mycorrhizal fungus inoculum potential in tropical deforested areas. *Mycorrhiza*, 32(1), 123 - 131.

López, C. L., Domic, A. I., Mayta, C., García, E., Quezada, J. A., & Gallegos, S. C. (2021). Pollen limitation and reproductive incompatibility system in a critically endangered tree, *Polylepis incarum* (Bitter) M. Kessler & Schmidt-Leb (Rosaceae). Neotropical Biodiversity, 7(1), 257-265.

López, C. L., Domic, A.I., Mayta, C., García, E. & S. Gallegos. 2018. Variaciones fenológicas de la Queñua (*Polylepis incarum*, Rosaceae) durante un ciclo annual en la puna mesofitica de La Paz, Bolivia. Ecología Austral. 8: 301-309.

Vega, C., JC. Bermejo., P. Rocabado., G. Villegas., J. Quezada & **C. L. López**. 2016. Proyecto IDH (2013-2014) “La keñua (*Polylepis*) árbol altoandino como alternativa ornamental para espacios verdes urbanos del Municipio de La Paz”. Unidad de Biotecnología Vegetal del Instituto de Biología Molecular y Biotecnología. Carrera de Biología. Facultad de Ciencias Puras y Naturales de la Universidad Mayor de San Andrés. IMP. ROTEMBOL. 1 ed. La Paz, Bolivia. 133 pp.

Papers under review and in advanced stages

Jiménez, E. A., **López, C. L.,** Fuentes, A. F., Hensen, I. & Gallegos, S. C. Influence of Pteridium fronds and leaf litter management on the soil seed bank characteristics in a fire-disturbed tropical montane forest. Submitted to *Biotropica* on 07.02.2025

Gallegos, S. C., **López, C. L.,** Kazuya, N., Solíz, C. A., Fuentes, A. F., Mayta, C., Cayola, L., Tello, S., & Hensen, I. A trait-based approach for restoring tropical forest in fire-deforested bracken-dominated areas. Submitted to *Journal of Applied Ecology* on 17.12.2024

Villegas, M., Mayta, C., **López, C. L.,** Maldonado-Alfaro, J. A., Hensen, I. & Gallegos, S. C. Scale-dependent responses of understory birds at the edges of forest remnants in a tropical Andean montane ecosystem. Under review in *Acta oecologica* since 13.07.2024

Mayta, C., Schleuning, M., **López, C. L.,** Villegas, M., Hensen, I., & Gallegos, S. C. Differences in bird and bat traits, seed-dispersal interactions and functions between tropical montane forest and bracken-dominated areas. Under review in *Frontiers in Ecology and Evolution* since 27.01.2025

Mayta, C., **López, C. L.,** Villegas, M., Hensen, I., & Gallegos, S. C. The use of bird perches and artificial bat roosts to overcome dispersal and establishment limitation in bracken-dominated deforested areas. Under review in *Biological conservation* since 25.03.2025

López, C. L., Mayta, C., Hensen, I. & Gallegos, S. C. Comparison of seed addition and seedling planting for the restoration of bracken-dominated areas under different management methods.

Conference contributions

López, C. L., Mayta, C., Solíz, C. A., Hensen, I. & Gallegos, S. C. (2025). The role of bracken fronds and litter on the performance of tree species. Facilitative or competitive effects?. *European Congress of Tropical Ecology (ECTE)*. Amsterdam, The Netherlands. (Poster).

López, C. L., Mayta, C., Fuentes, A. F., Villegas, M., Jiménez, E. A., Vasquez, V., Hensen, I. & Gallegos, S. C. (2023). Effect of bracken fern on natural plant recruitment in fire-deforested tropical mountain forests. V Bolivian Congress of Ecology. Cochabamba, Bolivia. (Talk).

López, C. L., Mayta, C., Hensen, I. & Gallegos, S. C. (2022). Different management strategies of *Pteridium* a trait bases approach. IV Bolivian Congress of Ecology. Santa Cruz, Bolivia. (Talk).

López, C. L., Mayta, C., Naoki, K., Quezada, J. A., Hensen, I., & Gallegos, S. C. (2021). The microbiota associated to *Pteridium* promotes the growth and survival of tree seedlings. First Bolivian Congress on Ecological Restoration. (Talk).

López, C. L., Domic, A. I., Palabral, A., Mayta, C., & Gómez, I. Effects of fungal infection by *Leptosphaeria polylepidis* on the demography of *Polylepis tarapacana* in the Sajama National Park, Bolivia. V Congress of ecology and conservation of *Polylepis* forests. Quito, Ecuador. (Poster).

López, C. L., Domic, A. I., Mayta, C., García, E., Quezada, J. A., & Gallegos, S. C. (2019). Reproductive incompatibility and pollen limitation system of Polylepis incarum (Rosaceae), an endemic and critically endangered species of the Lake Titicaca basin. V Congress of ecology and conservation of *Polylepis* forests. Quito, Ecuador. (Talk).

López, C. L., Domic, A. I., Mayta, C., García, E., Quezada, J. A., & Gallegos, S. C. (2016). Reproductive phenology of Polylepis incarum in an annual cycle. IV Congress of ecology and conservation of Polylepis forests. Jujuy, Argentina. (Talk).

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „The role of bracken's fronds and litter on tree seedling performance in a tropical montane forest: a trait based approach“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Cecilia Lorena López Alípaz, Halle (Saale),