Factors limiting forest regeneration in bracken-dominated areas in the tropical montane forest of Bolivia

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2014

Cover photo

Tropical montane forest edge and degraded habitat dominated by bracken in Bolivia (photo by S.C. Gallegos)

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Dissertation

zur Erlangung des
Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

der

Naturwissenschaftlichen Fakultät I – Biowissenschaften –

der Martin-Luther-Universität
Halle-Wittenberg,

vorgelegt

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geboren am 14. September 1981 in La Paz, Bolivia

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Halle (Saale), 2.12.2014

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Summary

Tropical forest biodiversity and ecosystem services are threatened by deforestation, converting continuous forests into fragmented remnants surrounded by degraded habitats. Forest regeneration is frequently hindered by human-induced fires. After fire, bracken fern (*Pteridium* spp.) often colonizes and persists in the degraded habitats for long periods. Previous studies suggested that bracken inhibits tree seedling recruitment. Therefore, most restoration policies to enhance forest regeneration in these areas applied a bracken removal management as well as seed addition and seedling transplantation of early-successional species. However, few studies focused on understanding the ecological processes involved in forest regeneration. Particularly, studies assessing seed and establishment limitation in bracken-dominated areas are scarce. Since plant life cycle encompasses different processes including seed dispersal, seed germination, seedling recruitment and adult establishment, abiotic and biotic factors that influence these processes will affect plant regeneration. To assess the effect of bracken on forest regeneration, sufficient ecological knowledge about the factors limiting forest recovery is critical to select the most efficient restoration strategy.

This thesis aims to investigate the main limiting factors on forest regeneration in bracken-dominated areas in the montane forest of Bolivia, by evaluating the relative importance of seed limitation and establishment limitation on seedling recruitment of forest species. I assessed seed limitation by analysing seed predation and the effect of secondary dispersal on seed predation, and studying species richness of forest seedlings. I assessed establishment limitation by analysing the effect of secondary dispersal on seedling recruitment and quantifying seedling survival and growth of three late-successional *Clusia* species as well as the naturally recruiting plant community. The thesis comprises three experimental studies. In the first study, I investigated seed predation and the effect of secondary dispersal on seed predation, germination and seedling recruitment of a primarily bird-dispersed large-seeded species, *Clusia trochiformis*. The main seed predators were vertebrates and the main secondary dispersers were ants. Ants often dispersed seeds beneath the litter layer and this directed dispersal reduced seed limitation by reducing predation risk, and reduced establishment limitation by dispersing seeds to specific microhabitats enhancing their probabilities of recruitment. In the second study, I investigated the effect of bracken fronds (above-ground vegetation) and litter on seedling recruitment, survival and growth of three shade-tolerant *Clusia* species. Bracken fronds and litter increased seedling recruitment and survival of the three species. These results suggest that bracken facilitates seedling recruitment of shade-tolerant species by ameliorating environmental conditions, arguing against an establishment limitation. In the third study, I evaluated the relative importance of seed limitation and establishment limitation on natural forest regeneration. I investigated species richness and the effects of bracken fronds on seedling recruitment, survival and growth at the community level, considering forest and non-forest species. Species richness of forest species decreased with increasing distance from the forest edge, highlighting the effect of seed dispersal limitation. Seedling survival and growth of forest and non-forest species were higher in the presence of bracken fronds, suggesting that bracken fronds facilitate seedling recruitment at the community level, and that there is only weak establishment limitation in the degraded areas.

There is no doubt that forest regeneration in bracken-dominated areas is slow. However, the present study shows that forest regeneration is hindered by seed limitation, related to the lack of animal-mediated seed dispersal, and not by establishment limitation. Furthermore, bracken facilitated seedling recruitment at the population and community levels, by ameliorating microclimatic conditions, contrasting to previous studies on the potential negative effect of bracken. The results underscore the importance of ecological knowledge for management recommendations. This study shows that seed addition of shade-tolerant late-successional species into the bracken vegetation could represent an efficient and cost-effective restoration practice to enhance the regeneration of tropical montane forest in bracken-dominated areas. However, due to their ecology, it is expected that late-successional species will take a long time to grow, but once established the community would already constitute late-successional vegetation that will persist for long periods. Seed addition of ant attractant seeds could enhance the effectiveness of the restoration efforts. Long-term studies will be needed to monitor the effectiveness of these practices.

Zusammenfassung

Die großflächige Abholzung tropischer Wälder bedroht die Artenvielfalt und Ökosystemdienstleistrungen. Kontinuierliche Wälder werden in Waldfragmente konvertiert, welche von degradierten Habitaten umgeben sind. Die Waldregeneration in den degradierten Flächen wird häufig durch von Menschen verursachte Brände behindert. Die gebrannten Flächen werden dabei häufig von Adlerfarn (*Pteridium* spp.) besiedelt, welcher für längere Zeit in diesen degradierten Flächen verbleibt. Ergebnisse frühere Studien deuten darauf hin, dass fehlende Samenausbreitung und Adlerfarn die Etablierung von Waldarten in den Flächen verhindert. Die meisten Renaturierungsmaßnahmen bestehen daher aus der Beseitigung des Adlerfarns zusammen mit der Ansaat oder Anpflanzung von Arten früher Sukzessionsstadien. Nur wenige Studien konzentrierten sich allerdings auf die ökologischen Prozesse, welche die Waldregeneration steuern. Besonders Studien, welche limitierte Samenverfügbarkeit und Etablierungschancen untersuchen, fehlen. Der Pflanzen-Lebenszyklus wird von verschieden Prozessen der Samenausbreitung, der Keimung sowie dem Wachstum bestimmt. Biotische und abiotische Faktoren welche diese Prozesse steuern bedingen folglich auch die Pflanzenregeneration. Um geeignete Sanierungsmaßnahmen vorzuschlagen, ist eine ausreichende Kenntnisse der ökologischen Faktoren eine wichtige Voraussetzung,

Die vorliegende Arbeit zielt darauf ab, die wichtigsten begrenzenden Faktoren der Waldregeneration in adlerfarn-dominierten Gebieten im bolivianischen Bergwald zu untersuchen. Der Fokus lag auf den Mechanismen der Samen- und Etablierungslimitierung. Es wurden die Prädation und die sekundäre Ausbreitung von Samen, sowie deren Keimung untersucht. Die Untersuchungen umfassten zum einen die gesamte Pflanzengemeinschaft sowie drei Arten später Sukzessionsstadien (*Clusia* spp.). Die Arbeit umfasst drei Experimente. In der ersten Studie wurde die Samenprädation sowie die Effekte der sekundären Samenausbreitung auf die Prädation, Keimung und Etablierung einer vogelausgebreiteten, großsamigen Art (*Clusia trochiformis)* untersucht. Vertebraten waren die Haupt-Prädatoren, Ameisen die Haupt-Verbreiter. Die sekundär ausgebreiteten Samen wurden häufig unter der Streuschicht ablegt, was das Prädationsrisiko senkte und die Etablierungschangen

dieser Samen erhöhte. In der zweiten Studie wurden die Effekte von Adlerfarn-Beschattung und Adlerfarn-Streu auf die Keimung, das Wachstum und das Überleben von drei schattentoleranten Arten der Gattung *Clusia* untersucht. Sowohl die Beschattung als auch die Adlerfarn-Streu erhöhten die Keimung und die Überlebenschancen aller drei untersuchten Arten. Die Ergebnisse deuten an, dass Adlerfarn die Keimung und Etablierung schatten-toleranter Arten unterstützt. In der dritten Studie wurden die relativen Effekte von Samen- und Etablierungslimitation auf die natürliche Waldregeneration untersucht. Der Einfluss der Entfernung zum Waldrand auf die Artenvielfalt sowie die Effekte des Adlerfarns auf die Keimung, das Wachstum und das Überleben wurden analysiert. Der Artenreichtum an Waldarten in den Brandflächen nahm mit zunehmender Entfernung zum Waldrand ab. Wachstum und Überleben waren höher im Beisein von Adlerfarn, was auf einen unterstützenden Effekt des Adlerfarns hinweist.

Die Waldregeneration in den adlerfarn-dominierten Flächen war langsam. Jedoch zeigt die vorliegende Studie, dass die Waldregeneration eher durch Samen- als durch Etablierungslimitierung vermindert ist. Adlerfarn unterstützte die Keimung und das Wachstum auf Populations- und Gemeinschaftsebene durch eine Verbesserung der mikroklimatischen Bedingungen. Dies steht im Gegensatz zu den Ergebnissen bisheriger Studien, welche größtenteils negative Effekte von Adlerfarn berichteten. Die Ergebnisse unterstreichen die Bedeutung des ökologischen Wissens für Managementempfehlungen. Die Aussaat von schatten-toleranten Arten könnte eine effiziente und kostengünstige Methode darstellen, um die Regeneration von tropischem Bergwald in adlerfarn-dominierten Flächen zu unterstützen. Jedoch sollten die langsamen Wachstumsraten dieser Arten berücksichtigt werden. Die Verwendung von Arten deren Samen Ameisen anlocken, könnte die Effektivität dieser Maßnahmen erhöhen. Langzeit Studien werden jedoch gebraucht, um Aussagen über die Wirksamkeit dieser Sanierungsmaßnahmen machen zu können.

Resumen

La biodiversidad y los servicios ecosistémicos que brinda el bosque tropical estan siendo amenazados por la deforestación, fragmentando bosques continuos hasta convertirlos en hábitats altamente degradados. A su vez, prácticas de quema ocasionadas por el hombre dificultan la regeneración del bosque y su recuperación gradual. Después del fuego, el helecho *Pteridium* (comúnmente conocido como: chusi, helecho macho, helecho hembra, helecho águila, helecho marranero, samambaia [portugués], bracken [inglés]) coloniza y se establece en estas áreas degradadas, dominando la vegetación por mucho tiempo. Estudios previos sugieren que *Pteridium* inhibe el reclutamiento de árboles, obstaculizando la regeneración del bosque con especies que caracterizaron el mismo. Por lo tanto, gran parte de las políticas de restauración para acelerar la regeneración de bosques en áreas dominadas por *Pteridium*, incluyen, como herramienta de manejo, la eliminación de la vegetación de las zonas a ser restauradas, la adición de semillas y/o el transplante de plántulas de especies de sucesión temprana y crecimiento rápido. Sin embargo, hasta la fecha, pocos estudios se han enfocado en identificar y comprender aquellos procesos ecológicos que intervienen en la regeneración del bosque tropical en áreas afectadas por el fuego. Entre los más importantes, están aquellos relacionados con la limitación tanto en la dispersión de semillas como en el establecimiento de plantulas en las zonas mencionadas, aunque sus estudios son aún escasos. Para investigar el efecto de *Pteridium* sobre la regeneración del bosque, es fundamental tener un conocimiento ecológico sobre los factores que limitan la recuperación del bosque, para de esta manera poder establecer estrategias de restauración más eficientes.

El objetivo de ésta tesis es investigar los principales factores que limitan la regeneración del bosque en áreas dominadas por *Pteridium* en el bosque montano de los Yungas de Bolivia, evaluando la importancia relativa de la limitación de semillas y de la limitación durante el establecimiento, en el reclutamiento de especies del bosque. Evalué la depredación de semillas y el efecto de la dispersión secundaria en la depredación de semillas, además de la variación en la riqueza de especies del bosque con la distancia al borde para estudiar aquellos factores que podrían estar actuando sobre la limitación de semillas. En cuanto al establecimiento, analicé el efecto de la dispersión secundaria de semillas en el reclutamiento de plántulas y cuantifiqué la sobrevivencia y el crecimiento de plántulas, tomando en cuenta tres especies de árboles de sucesión tardía (tolerantes a la sombra) del género *Clusia* para estudiar su incidencia a nivel poblacional y considerando el reclutamiento natural de plántulas en el área, para su evaluación a nivel de comunidades. La tesis comprende tres estudios experimentales. En el primero, investigué la depredación de semillas y el efecto de la dispersión secundaria en la depredación, germinación y reclutamiento de semillas de *Clusia trochiformis*, una especie con semillas grandes cuyos dispersores primarios son aves. Los resultados mostraron que los principales depredadores de semillas fueron vertebrados, mientras que los dispersores secundarios más importantes fueron hormigas, las cuales dispersaron las semillas, en su mayoría, bajo la hojarasca. Esta forma de dispersión dirigida redujo la limitación de semillas al disminuir el riesgo de predación, y disminuyó la limitación durante el establecimiento al dispersar las semillas hacia microhábitats específicos incrementando sus probabilidades de reclutamiento. En el segundo estudio, investigué el efecto de las frondas (vegetación encima del suelo) y hojarasca de *Pteridium* en el reclutamiento, sobrevivencia y crecimiento de plántulas de tres especies tolerantes a la sombra del género *Clusia*. La vegetación y hojarasca de *Pteridium* aumentaron el reclutamiento y la sobrevivencia de las tres especies, por lo que estos resultados sugieren que *Pteridium*, contrario a una posible limitación para el establecimiento de otras plantas, facilita el reclutamiento de especies tolerantes a la sombra, al mejorar las condiciones ambientales extremas. En el tercer estudio, evalué la importancia relativa de la limitación de semillas y de la limitación durante el establecimiento en la regeneración natural del bosque. Investigué la riqueza de especies y el efecto de la vegetación de *Pteridium* en el reclutamiento, sobrevivencia y crecimiento de plántulas a nivel de comunidades, considerando especies características del bosque y de ambientes degradados (no-bosque). Los resultados obtenidos evidencian que la riqueza de especies del bosque disminuyó con el aumento de la distancia desde el borde del bosque hacia el área degradada, reflejando la limitación que existe en cuanto a la dispersión de semillas. La sobrevivencia y crecimiento de especies tanto características como ajenas al bosque, fueron mayores en presencia de vegetación de *Pteridium*, sugiriendo que la presencia de *Pteridium* facilita el reclutamiento de plántulas a nivel de la comunidad, y que solo existiría una leve limitación durante el establecimiento, en estas áreas.

No hay duda sobre la lentitud en la regeneración del bosque en áreas dominadas por *Pteridium*. Sin embargo, el presente estudio muestra que la regeneración del bosque se ve dificultada por la limitación de semillas ligada a la falta de dispersión de semillas por animales, y no por una limitación durante el establecimiento. Además, *Pteridium* facilitó el reclutamiento de semillas tanto a nivel de poblaciones como de comunidades, al mejorar las condiciones microclimáticas, contrastando previos estudios sobre el potencial efecto negativo de *Pteridium*. Los resultados subrayan la importancia del conocimiento ecológico para recomendaciones de manejo. Este estudio muestra que la adición de semillas de especies tolerantes a la sombra directamente en la vegetación dominada por *Pteridium*, podría representar una práctica eficiente y costo-efectiva de restauración para promover la regeneración del bosque montano tropical en áreas dominadas por *Pteridium*. Después de su establecimiento, la comunidad estaría constituida directamente por vegetación de sucesión tardía, la cual podría persistir por largos periodos de tiempo. Además, la adición de semillas que atraen hormigas podría aumentar la eficacia de los esfuerzos en restauración. Estudios a largo plazo serán necesarios para monitorear la efectividad de dichas prácticas.

Chapter 1. General introduction

Biological processes and influencing factors

The plant life cycle encompasses many biological processes including seed production, seed dispersal, germination, seedling recruitment and the establishment of an adult plant (Fig. 1). Different biotic and abiotic factors influence these processes and determine the successful establishment of a new plant. *Seed dispersal* links the end of the reproductive cycle with the beginning of the establishment of the offspring (Wang & Smith 2002). Most tropical forest tree species are dispersed by animals (i.e., are zoochorous; Howe & Smallwood 1982). Therefore, animal dispersal represents the most important form of seed dissemination in these forests (Howe & Smallwood 1982). The seed dispersal process affects seed germination, predation, establishment, and defines where the new individual is going to grow, develop, reproduce and die (Nathan & Muller-Landau 2000; Wang & Smith 2002). Seed dispersal is considered effective when the seeds are not only dispersed, but when it also results in successful plant establishment (Schupp, Jordano & Gómez 2010). Seed dispersal often constitutes several consecutive steps by different animals. The combination of different dispersal mechanisms often increases the probability of seed germination (Vander Wall & Longland 2004). Primary seed dispersers, typically birds and mammals, move the seeds from the parent plant to the first deposition site (Fig. 1; Vander Wall & Longland 2004; Vander Wall, Kuhn & Gworek 2005b). Primary dispersers move seeds over long distances, reducing density-dependent mortality near the parent plant, and have little effect on directing seeds to favourable microhabitats for establishment (Vander Wall & Longland 2004; Schupp *et al.* 2010). Secondary dispersers, such as ants, dung beetles and scatter-hoarding rodents, move the seeds from the first deposition site to a second (or third) deposition site (Fig. 1; Vander Wall 1993; Passos & Oliveira 2002; Lawson, Mann & Lewis 2012). Secondary dispersers usually move seeds for small distances, but often direct seeds to favourable microhabitats for germination and establishment (i.e., directed seed dispersal; Wenny 1999; Passos & Oliveira 2002; Briggs, Vander Wall & Jenkins 2009). Although secondary dispersers frequently forage on seeds, they often scatter or bury them reducing the probability of seed predation (Wenny 1999; Vander Wall & Longland 2004).

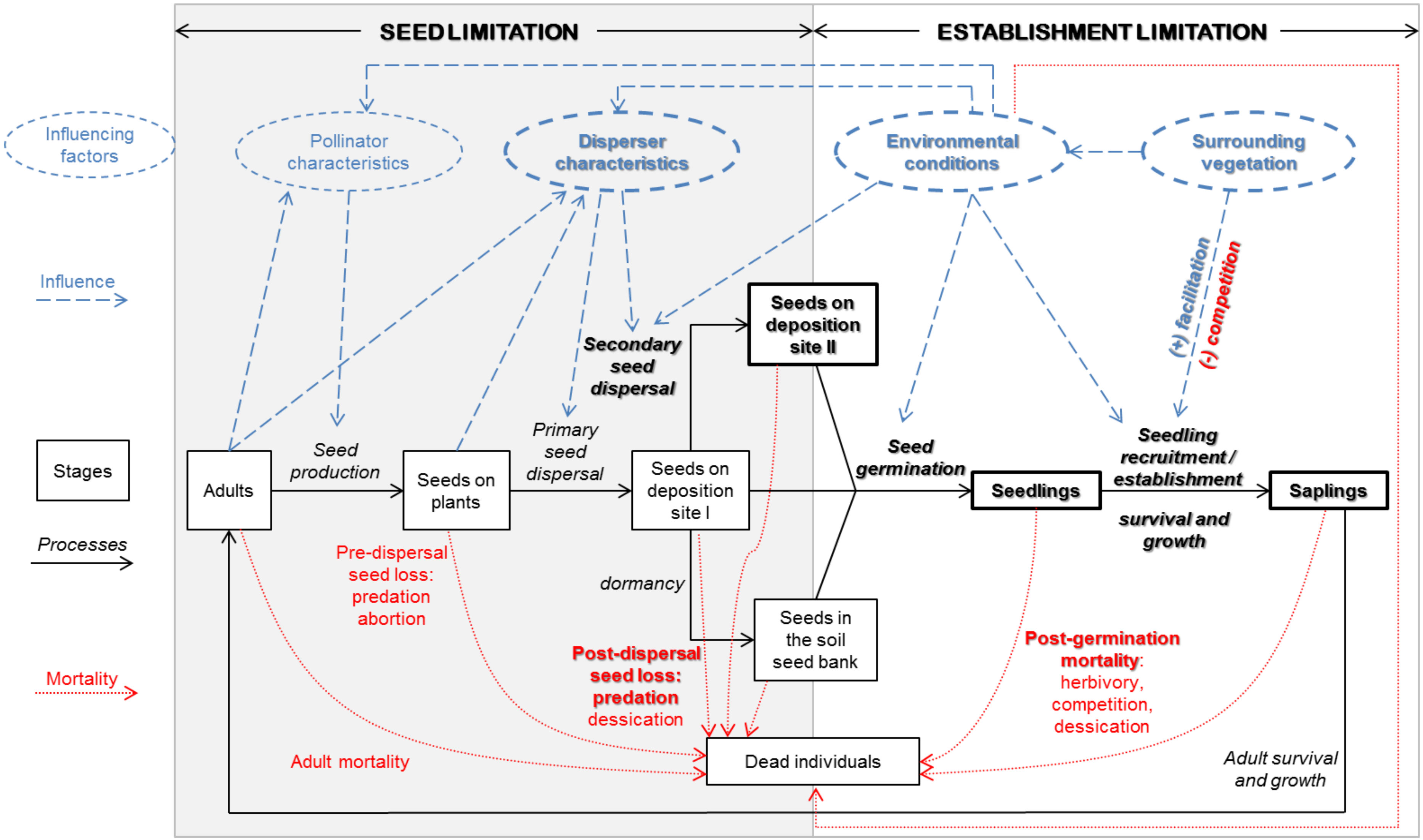

Figure 1. The biological processes and influencing factors involved during the plant life cycle indicating the stages and processes affected by seed and establishment limitation. The stages, processes and influencing factors considered in this study are denoted in bold. Modified from Nathan & Muller-Landau 2000.

Post-dispersal seed predation is one of the main causes of seed loss (Hulme 1998; Myster 2004). The main post-dispersal seed predators are rodents and ants (Hulme 1998). In some cases, ants can have a dual role acting as seed predators and dispersers (Levey & Byrne 1993). While small mammals tend to show higher seed predation when the vegetation cover is high, ants tend to forage more often in open habitats (reviewed by Hulme 1998). Seed preferences of predators depend on the characteristics of the seed predators (body size, olfactory acuity, hunger), the seeds (seed size, shape, nutrient contents), and the environment (vegetation cover, food abundance, soil characteristics; Hulme 1998).

After seed arrival, seeds can be either stored in the soil, constituting the *seed bank*, or *germinate* within a few days or weeks. The time for seed germination mainly depends on the environmental conditions and seed characteristics. Seeds with the ability to persist in the seed bank, denominated dormant seeds, are tolerant to dehydration or desiccation and can remain viable in the soil for long periods. Dormant seeds are sensitive to light (Foster & Janson 1985; Vázquez-Yanes & Orozco-Segovia 1993), and germinate only when suitable environmental conditions develop (e.g., high red/far-red light ratios, and diurnal fluctuating temperatures; Vázquez-Yanes & Orozco-Segovia 1993). In the tropics, the seed bank is dominated by small-seeded species (Garwood 1989; Dalling, Swaine & Garwood 1997). Seeds that are not able to persist in the seed bank, denominated non-dormant seeds, are highly sensitive to desiccation and usually germinate soon after dispersal or quickly lose their viability (Bazzaz & Pickett 1980).

Seed characteristics determine the regeneration strategy of species. Seed mass is a key ecological trait because it can be correlated with shade-tolerance, seed and seedling survival, plant height, growth form and dispersal syndrome, among other important aspects of the regeneration strategy (Leishman *et al.* 2000; Moles & Westoby 2004). In contrast to small-seeded species, including most early-successional (or pioneer) and non-forest species, most large-seeded species are late-successional (i.e., non-pioneer, typical of mature forests), dispersed by animals, shade-tolerant, litter tolerant, have high moisture and nutrient contents, germinate rapidly after dispersal (i.e., do not persist in the soil seed bank) and therefore have rapid establishment and invest less in protection against seed predators (Bazzaz &

Pickett 1980; Swaine & Whitmore 1988; Facelli & Pickett 1991; Vázquez-Yanes & Orozco-Segovia 1993; Leishman *et al.* 2000; Moles & Westoby 2004; Berjak & Pammenter 2008; Table 1).

Most tree species show a trade-off between growth rates and survival, especially during early life stages (Kitajima 1994; Poorter & Bongers 2006; Poorter *et al.* 2008). While large-seeded species have low growth rates and high survival, small-seeded species are characterized by high growth rates and low seedling survival (Poorter & Rose 2005). It has been proven that large-seeded species have an advantage against small-seeded species and are better adapted to survive under severe conditions because they have a higher tolerance to a wide variety of hazards (Leishman *et al.* 2000). The advantages of large-seeded species are related to their higher seed reserves, larger seedling sizes, and carbohydrate allocation to storage in the seedling and sapling stages (Kobe 1997; Leishman *et al.* 2000; Poorter *et al.* 2008). Large-seeded species also have a higher performance as adults (Poorter *et al.* 2008). In adult trees of these species, growth rates increase and mortality rates decrease with an increase in stature because taller species have greater access to light and a longer life span (Poorter *et al.* 2008).

Since seedlings deal with a variety of hazards during establishment, mainly related to the influence of environmental conditions and the surrounding vegetation (Fig. 1), natural selection may operate strongly during the early life stage of plants (Leishman *et al.* 2000). Seeds and seedlings experience high mortality after dispersal (Augspurger & Kitajima 1992; Hammond 1995; Rother *et al.* 2013). Thus, seedling recruitment constitutes a bottleneck in population dynamics (Poorter 2007; Baldeck *et al.* 2013). However, seedling growth and survival often remain stable after the first year (Augspurger & Kitajima 1992; Baraloto, Forget & Goldberg 2005; Martínez-Garza, Bongers & Poorter 2013). Consequently, studies of early seedling stage have high potential to predict plant performance for longer periods (Martínez-Garza *et al.* 2013).

Table 1. Some typical characteristics of early and late-successional species. Note that not all species within groups contain all of these characteristics.

Characteristic	Early successional, pioneer or light-demanding species	Late successional, non-pioneer or shade-tolerant species
seed size	small	large
seed number	high	low
main dispersal syndrome	anemochory (wind)	zoochory (animals)
light requirements for germination	high	low
seeds stored in the soil seed bank	yes	no
seeds light sensitive	yes	no
seeds litter tolerant	no	yes
seedling survival	low	high
seedling growth rate	high	low
seedling tolerance to severe conditions	low	high
sapling survival	low	high
life span	short	long

Based on: Bazzaz & Pickett 1980; Foster 1986; Swaine & Whitmore 1988; Facelli & Pickett 1991; Vázquez-Yanes & Orozco-Segovia 1993; Vander Wall 1995; Leishman *et al.* 2000; Moles & Westoby 2004; Berjak & Pammenter 2008; Wang & Chen 2009.

Tropical forests: disturbance and regeneration

Tropical forests harbour the highest biodiversity in the world (Mittermeier *et al.* 2011; Pimm *et al.* 2014). However, high land-use and land-cover changes are threatening the large biodiversity and ecosystem services provided by these forests (Pimm & Sugden 1994; Foley *et al.* 2005; Pimm *et al.* 2014). Fire-clearing of forest for land-use activities such as cattle grazing, logging and agriculture, transform large proportions of forest into fragmented patches surrounded by disturbed vegetation (Holl 2002; Chazdon *et al.* 2007). In most cases, disturbed areas exhibit low-growing and often open vegetation dominated by grasses or ruderal weeds, with low structural complexity and diversity (Denslow & Guzman 2000; Holl 2002; Capers *et al.* 2005). Therefore, forest regeneration is necessary to restore many components of the biodiversity and ecosystem services after disturbance (Chazdon 2008).

Natural forest regeneration in disturbed habitats is a successional process from pioneer communities composed of early-successional species, which would be subsequently replaced by late-successional species (Bazzaz 1979). The successional process is influenced by many abiotic and biotic mechanisms (Connell

& Slatyer 1977; Pickett, Collins & Armesto 1987). Natural regeneration of the forest in disturbed areas depends on, among other things, the frequency and intensity of disturbance (Holl & Aide 2011). After small disturbances (e.g., logging and silvicultural practices), the areas can be quickly colonized by species within the soil seed bank and other nearby seed sources, mainly by small-seeded species (Finegan & Camacho 1999), and thus regenerate in a relatively short amount of time (e.g., Uhl, Buschbacher & Serrao 1988; Aide *et al.* 2000; Carreño-Rocabado *et al.* 2012) . In contrast, after intensive disturbances (e.g., frequent fires, abandoned agricultural lands) the seed bank is often destroyed or depleted of forest species (e.g., Nepstad *et al.* 1996; Zimmerman, Pascarella & Aide 2000). Seed colonization of these areas is restricted to forest sources nearby or non-forest ruderal and invasive species quickly colonize and often dominate the area. Therefore, forest regeneration in intensively disturbed areas is often slow (reviewed by Holl 2002).

The main factors limiting forest regeneration in most disturbed areas are *seed limitation* due to the scarce seed dispersal into disturbed areas and high seed predation, and *establishment limitation* due to the harsh abiotic conditions and competition with the surrounding vegetation (Fig. 1), which inhibit seed germination, seedling survival and/or growth (reviewed by Holl 1999, 2012; Holl *et al.* 2000). Seed limitation in disturbed areas in the tropics is mainly associated with the high number of species that depend on animals for seed dispersal (Howe & Smallwood 1982; Wunderle 1997). The low seed dispersal into disturbed areas is related to the low availability of perches, structural complexity and food resources for attracting animal seed dispersers (Wunderle 1997). Seed limitation is also associated with high seed predation rates in disturbed habitats (Uhl 1987; Aide & Cavelier 1994; Holl & Lulow 1997).

Forest regeneration also depends on environmental factors in the disturbed areas, influenced by the vegetation structure, and determine when, where and which species can regenerate (Lebrija-Trejos *et al.* 2010, 2011). Environmental factors vary in space and different species will be able to recruit only in certain microhabitats within a habitat (Bazzaz 1996). Environmental conditions in disturbed areas are characterized by higher temperatures and irradiance, and lower humidity and soil moisture compared to forests (Holl 1999; Loik & Holl 1999; Lebrija-Trejos *et al.*

2011). The harsh environmental conditions in disturbed areas may limit the succession because most forest species are not adapted to such conditions, constituting an establishment limitation. The establishment limitation can be also related to the surrounding vegetation, which can have positive (facilitative) or negative (competitive) effects on seedling establishment (Connell & Slatyer 1977; Pickett *et al.* 1987). Under harsh environmental conditions, facilitation and competition determine the recovery rates of disturbed areas. The stress-gradient hypothesis predicts that facilitation increases under high abiotic stress, while competition increases when abiotic stress is low (Bertness & Callaway 1994; Callaway & Walker 1997; Maestre *et al.* 2009). Accordingly, facilitation is more likely to occur during early-successional stages, when only few species can cope with the harsh abiotic conditions (Connell & Slatyer 1977). Facilitation in disturbed areas of tropical moist forests might be important because species adapted to moist ecosystems have relatively low drought tolerance (Holmgren & Scheffer 2010). Many studies in disturbed habitats demonstrated that some shrubs and trees facilitate seedling establishment of forest species by improving the conditions beneath their canopies (e.g., Chapman *et al.* 2002; Gómez-Aparicio 2009; Salazar *et al.* 2012; Avendaño-Yáñez *et al.* 2014). In contrast, many studies showed that some grasses, weeds and ferns compete for soil moisture, nutrients and/or light with forest species (e.g., Holl *et al.* 2000; Zimmerman *et al.* 2000; Slocum *et al.* 2004). However, in many cases the results depend on the life history of the species involved (Maestre *et al.* 2009; Gómez-Aparicio 2009).

Fire and the bracken fern

Slash-and-burn practices and unintended human-induced fires are common in the tropics (Aide *et al.* 2000; Cochrane 2003; Holl 2012), fragmenting the landscape into forest patches surrounded by abandoned fire-degraded habitats. Understanding the processes that influence the regeneration of fire-degraded areas is an important field in applied ecology (Lamb, Erskine & Parrotta 2005). Sufficient ecological knowledge about the factors limiting forest recovery is critical to select the most efficient restoration strategy (Holl & Aide 2011). After fire, bracken fern often colonizes and dominates large areas and persists for long periods.

The bracken fern, *Pteridium* spp. (Dennstaedtiaceae), is a world-wide weed that occurs in all continents, except Antarctica, from sea level to above 3000 m (Marrs & Watt 2006; Der *et al.* 2009). Bracken responds to human disturbance, and often invades open areas after forest clearance, cultivation and especially fire (Marrs *et al.* 2000; Marrs & Watt 2006). Bracken constitutes a highly stable vegetation that can persist for long periods (Marrs *et al.* 2000; Beck, Hartig & Roos 2008; Roos *et al.* 2010b; Lippok *et al.* 2013a; Alday & Marrs 2014). Bracken can inhibit tree seedling establishment (e.g., Den Ouden 2000; Marrs *et al.* 2000; Silva Matos & Belinato 2010), and thereby slow forest regeneration (Parrotta, Turnbull & Jones 1997; Marrs *et al.* 2000; Weber *et al.* 2008). The main reasons for bracken's success are: (i) a large rhizome system storing large amounts of carbohydrates and nutrients; (ii) rapid frond production (above-ground vegetation); (iii) a large and dense frond canopy that shades other species; (iv) large litter accumulation that inhibits other species from colonizing; (v) a large spore production that can be induced by fire; (vi) high chemical contents against herbivores and pathogens; and (vii) possible allelopathic effects (Marrs *et al.* 2000; Ghorbani *et al.* 2006; Marrs & Watt 2006; Robinson, Sheffield & Sharpe 2010; Ramírez-Trejo *et al.* 2010).

Many studies focused on bracken control. Most of the studies about bracken have been made in Europe, where the restoration policies focus on restoration of semi-natural communities of grasslands, heathlands and moorlands (Marrs *et al.* 2000, 2007; Alday *et al.* 2013; Alday & Marrs 2014). These practices represent a reverse-succession to early communities dominated by grasses, herbs and small shrubs (Marrs *et al.* 2000), which are suppressed by bracken due to their high light and low litter requirements. These studies used mechanical and chemical methods at different intensities to control the establishment of bracken. They concluded that frequent vegetation and litter removal, and seed addition of early-successional species are essential to restore grasslands, heathlands and moorlands (Lowday & Marrs 1992; Marrs *et al.* 2000; Stewart *et al.* 2008; Alday *et al.* 2013). However, none of them was able to eradicate bracken completely (Marrs *et al.* 2000; Alday *et al.* 2013). Although it was acknowledged that woodland could represent a more suitable target in many cases (Marrs *et al.* 2000; Tong *et al.* 2006), few studies attempted to increase woodland development (e.g., Humphrey & Swaine 1997; Den Ouden 2000; Priewasser 2013). Despite the observations of tree seedlings recruiting under bracken, it has been suggested that bracken vegetation and/or litter removal were needed to enhance the development of woodlands (reviewed by Marrs & Watt 2006).

The vast knowledge about the ecology of bracken in temperate regions could explain the scarcity of studies in the tropics (Miatto *et al.* 2011; Palomeque 2012). Although some researchers found that forest species richness of tropical trees is low in bracken-dominated areas (Günter *et al.* 2007; Palomeque 2012; Ribeiro *et al.* 2013; Lippok *et al.* 2013a), the factors limiting forest regeneration in these areas have received little attention (Palomeque 2012; Lippok *et al.* 2013a). The restoration activities in tropical bracken degraded areas have been normally focused on the establishment of fast growing species with economic importance, which are usually small-seeded, early-successional species that are outcompeted by bracken vegetation and litter (Aguirre *et al.* 2006; Weber *et al.* 2008; Günter *et al.* 2009). Therefore, most of the studies assumed a negative effect of bracken in degraded areas, and applied a mixture of strategies suggested from findings in the temperate zone and from pastures in the tropical zone (e.g., Günter *et al.* 2009; Silva Matos & Belinato 2010; Avendaño-Yáñez *et al.* 2014). Consequently, they frequently removed bracken vegetation and litter, and added early-successional seeds, or transplanted nursery raised seedlings of early and late-successional species (e.g., Weber *et al.* 2008; Günter *et al.* 2009; Silva Matos & Belinato 2010; Douterlungne *et al.* 2010; Cole *et al.* 2011; Avendaño-Yáñez *et al.* 2014). To our knowledge, only one study succeeded in eradicating bracken by removing the vegetation every two weeks and seeding with *Ochroma pyramidale,* an early-successional tree species (Douterlungne *et al.* 2010; Douterlungne & Thomas 2013). Due to its fast growth, *O. pyramidale* shaded-out bracken eliminating it after 18 months. Douterlungne and Thomas 2013 highlighted that elimination of bracken may be impossible if it is not shaded-out. However, the high costs involved for the intensive bracken removal treatment may be difficult to cover. Additionally, it has recently been suggested that the establishment of late-successional tree species in *O. pyramidale* secondary forests is low, decreasing successional development (Vleut *et al.* 2013).

Study objectives

To understand the limiting factors on forest regeneration, it is important to investigate the key ecological processes involved during the plant life cycle of forest species and the factors influencing these processes. Although each of these processes is important, seeds and seedlings represent the most susceptible stages, especially in disturbed habitats. Therefore I will concentrate on some of the key processes, from seed arrival to seedling recruitment, and key influencing factors, including environmental conditions and interactions with the surrounding vegetation, affecting forest regeneration (Fig. 1).

The aim of my thesis was to investigate the main limiting factors on forest regeneration in bracken-dominated areas in the montane forest of Bolivia, by evaluating the relative importance of seed limitation and establishment limitation on seedling recruitment of forest species. I assessed the influence of seed predation and secondary seed dispersal on forest regeneration, and the effect of bracken on seedling establishment of three late-successional species and the naturally recruiting plant community. The thesis comprises three experimental studies (Chapters 2-4) comparing the processes in the forest interior and bracken degraded habitats.

The first study (**Chapter 2**) investigated the effects of secondary seed dispersal on seed predation, germination and seedling recruitment of a primarily bird-dispersed large-seeded species, *Clusia trochiformis*. I investigated whether secondary dispersal contributes to forest regeneration by reducing seed predation and increasing seed germination and seedling recruitment. This study assessed the importance of secondary seed dispersal and seed predation on seed limitation. I conducted seed dispersal and predation experiments with marked seeds and vertebrate exclusions in the forest and in the degraded habitat. I analysed the effects of habitat type and animal guild on seed predation, secondary dispersal, germination and seedling recruitment. I found that secondary dispersal by ants increases the probability of seed germination and reduces the probability of seed predation in the degraded habitat. Seed predation in the degraded habitat was generally low. These findings highlight the importance of secondary dispersal for reducing seed limitation.

The second study (**Chapter 3**) aimed to determine the effect of bracken vegetation and litter on seedling recruitment, survival and growth of three late-successional species of *Clusia* (*C. trochiformis, C. lechleri* and *C. sphaerocarpa*). This study assessed the importance of bracken vegetation and litter on establishment limitation. I applied experimental treatments of vegetation and litter removal, in the forest and degraded habitat, and added *Clusia* seeds simulating natural dispersal conditions by spreading them into experimental plots. I tested the effects of vegetation and litter removal on seedling recruitment after three months and one year. The effects of bracken vegetation and litter removal were related to abiotic variables. I assessed the differences in recruitment of three *Clusia* species between the experimental treatments and habitat types and I found that seedling recruitment and survival were higher in presence of bracken vegetation and litter. This result suggests an amelioration of harsh environmental conditions and therefore, facilitation by bracken and a lack of establishment limitation.

The third study (**Chapter 4**) aimed to assess the combined effects of seed limitation and establishment limitation on natural forest regeneration in bracken-dominated areas. I experimentally assessed natural seedling recruitment, survival and growth at the community level, and performed a vegetation removal treatment to investigate the effect of bracken fronds on forest regeneration after two years. The study was conducted at different distances within the forest interior and degraded habitat. All recruiting seedlings were classified according to their habitat preference as forest and non-forest species. I analyzed the effect of vegetation removal, habitat preference and habitat type on species richness, seedling survival and growth. Additionally, in the degraded habitat, I evaluated the effect of distance to the forest edge, habitat preference and vegetation removal on species richness. This study assessed the effect of seed limitation on species richness of forest species seedlings in the degraded habitat. Establishment limitation was addressed by analyzing the effect of bracken fronds on seedling survival and growth. I found that species richness in the degraded habitat decreased with increasing distance from the forest edge, suggesting seed limitation. Furthermore, seedling survival and growth were higher in the presence of bracken fronds, suggesting a lack of establishment limitation.

Since deforestation and bracken infestation is widespread in the tropical region, the results of this thesis will contribute to a better understanding of the factors limiting tropical forest regeneration in bracken degraded habitats and have various implications for the restoration of degraded tropical montane forests.

Study area

The tropical mountain forest of the Andes harbours one of the main biodiversity hotspots in the world (Barthlott *et al.* 2005). The high biodiversity is related to important variation in climate, elevation, geology and soil characteristics along the Andes that produce large habitat and microhabitat heterogeneity (Homeier 2008; Richter 2008). The eastern slope of the Andes is characterized by a chain of humid mountains and valleys with variable morphology and a wide altitudinal gradient from ca. 400 to 3000 m of elevation (Beck, Killeen & García 1993). The vegetation in this belt is denominated as tropical montane forest or Yungas vegetation. The highest biodiversity is between 1500 and 2000 m, with peaks of endemism above 2000 m (Kessler & Kluge 2008). The highest endemism zone coincides with the areas with highest human impact (Kessler *et al.* 2001).

The study was conducted in the tropical montane forest of Bolivia between 1900 and 2500 m of elevation, in the vicinity of Chulumani village (16°24’ S, 67°31’ W), 120 km from La Paz city. Mean annual temperature is 20.8° C and mean annual precipitation is 1459 mm, with a peak between January and March (Molina-Carpio 2005). The forests around Chulumani are highly fragmented by frequent human-induced fires and the extension of coca (*Erythroxylum coca,* Erythroxylaceae) plantations (Killeen *et al.* 2005). Only two relicts of mature continuous forest, of ca. 3,000 ha each, persist in the study area (Fig. 2). The most important plant families in the forest are Lauraceae, Rubiaceae, Myrtaceae, Melastomataceae, Piperaceae and Euphorbiaceae; and the important species are: *Hedyosmum racemosum* (Chloranthaceae)*, Palicourea grandiflora* (Rubiaceae)*, Hieronyma moritziana* (Phyllanthaceae)*, Clusia sphaerocarpa* (Clusiaceae) and *Elaeagia mariae* (Rubiaceae) (Beck *et al.* 1993; Mueller, Beck & Lara 2002; Lippok *et al.* 2014). The forest relicts are surrounded by fire-degraded habitats (Fig. 3) dominated by the bracken fern *Pteridium arachnoideum* (Dennstaedtiaceae) accompanied by non-forest species of shrubs like *Chromolaena laevigata, Baccharis platypoda* (Asteraceae), *Tibouchina stenocarpa* (Melastomataceae) and *Collaea speciosa* (Fabaceae) (Lippok *et al.* 2013a). Bracken covers more than 70% of the vegetation in the degraded habitats, and most of the litter is also comprised of bracken (mean fronds height: approx. 1 m; depth of litter layer: 5-20 cm).

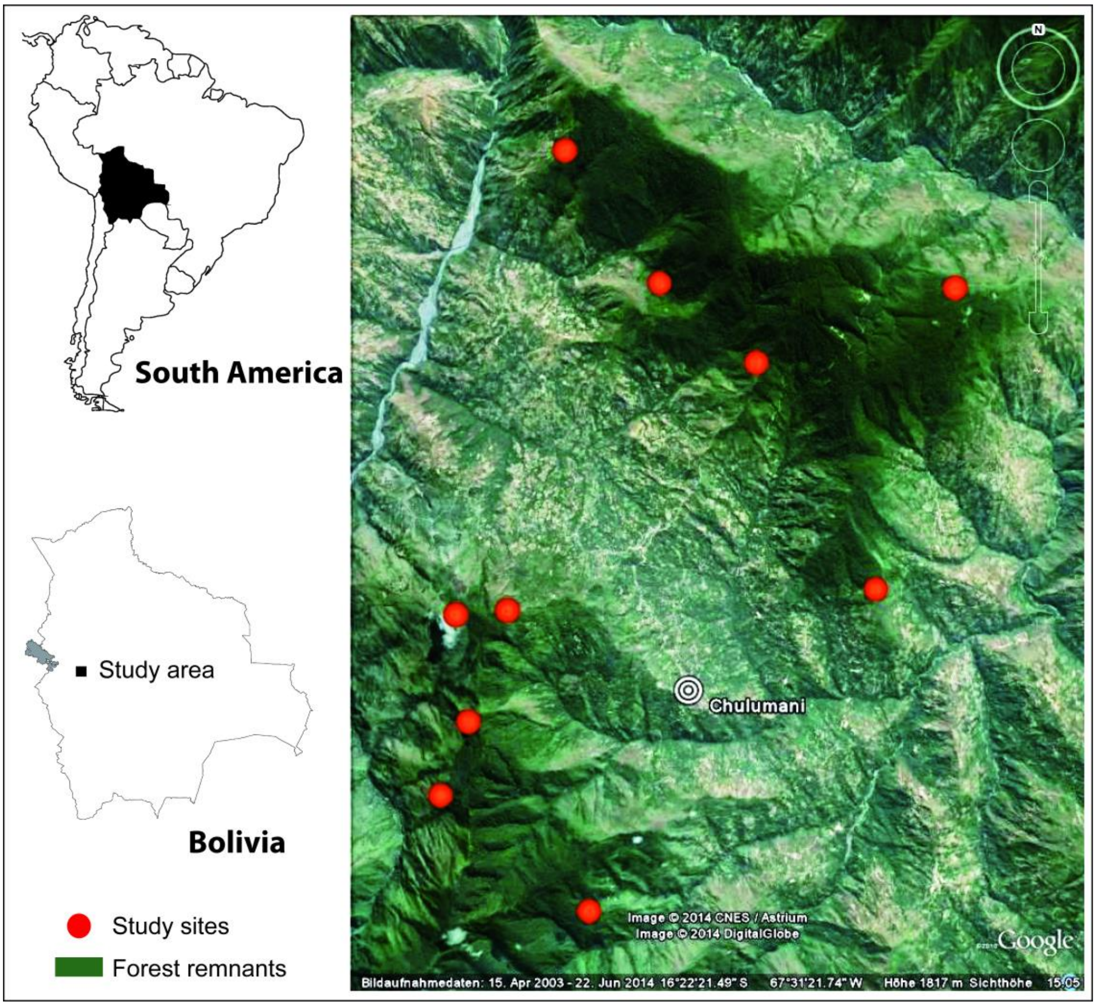

Figure 2. Map of the study area highlighting the two large forest remnants (dark green) and study sites.

Forest relicts in the area often have sharp borders between the forest interior and bracken degraded habitat (Fig. 3). I selected ten sites and I installed 240 m-long transects perpendicular to the forest edge (Fig. 3). The transects were set up to 160 m from the forest edge to the forest interior (because at this distance the forest had mature characteristics) and up to 80 m in the degraded habitat to compare the effects close and far from the forest edge. Along each transect, I selected seven distances: 160, 40, and 20 m in the forest interior, and 5, 20, 40 and 80 m in the degraded habitat. The three experiments were installed at specific distances, according to the respective objectives.

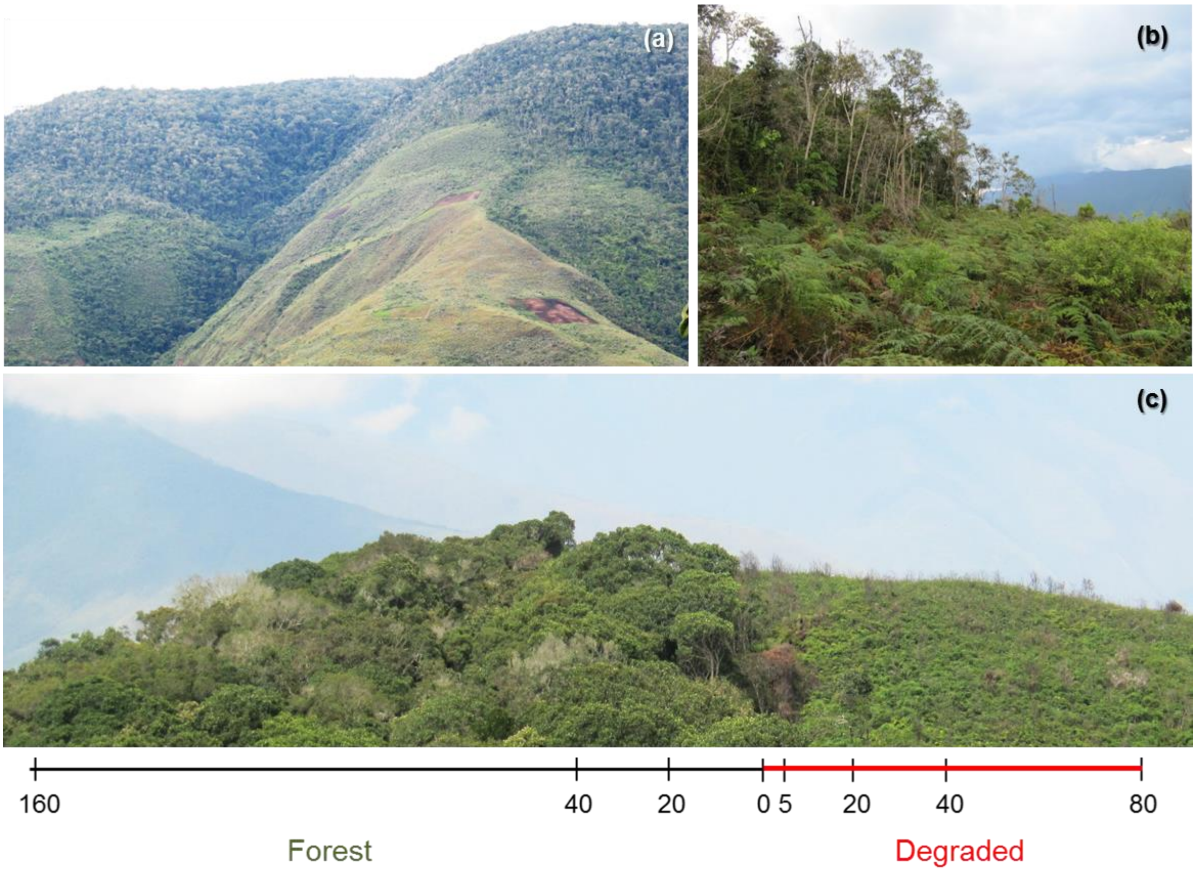

Figure 3. (a) Forest remnant surrounded by fire-degraded habitats; (b) detail of the sharp border between the forest and degraded habitat showing the dominance of bracken; (c) scheme of the transect arrangement.

Study species

I selected *Clusia* species as a model system because these species are common in tropical forests (Araujo & Scarano 2007). The *Clusia* L. (Clusiaceae) genus is distributed over Central and South America and occurs in a wide variety of habitats from tropical rain forest to savannas including secondary forests and fire-degraded habitats (Araujo & Scarano 2007; Lippok *et al.* 2013a). *Clusia* spp. are primarily dispersed by birds and secondarily dispersed by ants (Passos & Oliveira 2002;

Gustafsson, Winter & Bittrich 2007; Saavedra *et al.* 2014). As most of the late-successional moist tropical forest trees, they have large seeds that germinate shortly after dispersal and are shade-tolerant, but are also able to grow in open habitats (Lüttge 2007). After establishment, *Clusia* species can be important nurse plants, facilitating the growth of many species beneath their canopy (e.g., Dias & Scarano 2007; Correia, Dias & Scarano 2010).

Figure 4. Fruits and seedlings of *Clusia* species. (a-b) *C. sphaerocarpa*; (c-d) *C. lechleri*; (e-f) *C. trochiformis*; (g) size comparison of ripe fruits of *C. sphaerocarpa* (up), *C. lechleri* (middle) and *C. trochiformis* (down); and (h) detail of a ripe fruit of *C. trochiformis* with seeds surrounded by red arils.

Three species of *Clusia* trees occur in the forest of the study area: *C. sphaerocarpa* Planch. & Triana, *C. lechleri* Rusby and *C. trochiformis* Vesque (Fig. 4). The three species are dioecious. Fruits are globular capsules that dehisce to expose diaspores, i.e., seeds surrounded by a red lipid-rich aril (Fig. 4; see also appendix in Chapter 3), which attract birds that are their main primary seed dispersers (Saavedra *et al.* 2014). The three species germinated within one week at high rates (>95% in all cases) in laboratory germination experiments under day light and complete darkness demonstrating their shade-tolerance. *Clusia trochiformis* was used in the experiments in Chapter 2, and all three species were used in Chapter 3.

Chapter 2.

Secondary dispersal by ants promotes forest regeneration after deforestation

Journal of Ecology (2014) **102**, 659–666.

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Abstract

1. Many remnants of tropical forests are surrounded by deforested areas dominated by successional vegetation. Although secondary dispersal by scatter-hoarding rodents and ants may influence seed predation and seedling recruitment, very little is known about its importance in degraded forest ecosystems.

2. We studied the effects of secondary dispersal on seed predation, germination and seedling recruitment of the primarily bird-dispersed tree *Clusia trochiformis* in a tropical montane forest in Bolivia. We carried out exclosure experiments that allowed or excluded access to seeds by vertebrates in three habitat types (forest interior, degraded habitat close to and degraded habitat far from the forest margin) in a spatial block design at six sites. We offered a total of 1,440 seeds (both with and without an aril) and marked half of them with a thread to follow their fate after 48 h and after 1 month.

3. We found that secondary dispersal by ants was highest in the forest interior but was also frequent in degraded habitats close to and far from the forest edge. Secondary dispersal significantly increased seedling recruitment, particularly in the degraded habitats, probably because seeds were often dispersed to sites beneath the leaf litter. Recruitment success increased significantly with dispersal distance. High recruitment of secondarily dispersed seeds in the degraded habitat was due to the combined effect of reduced predation and increased germination of seeds that had been moved by ants.

4. *Synthesis*. In the absence of secondary dispersal, seed germination and seedling recruitment were very low in degraded habitats. Seed dispersal by ants substantially increased natural regeneration in the deforested habitats. Our experiments thus demonstrate that the effects of biotic interactions on plant demography can vary across habitat boundaries at small spatial scales and that secondary dispersal is a crucial and overlooked process that can aid the regeneration of deforested habitats in the tropics.

Keywords: aril, *Clusia*, directed dispersal, forest regeneration, germination, human disturbance, plant-animal interactions, plant population and community dynamics, seed predation, tropical forest

Chapter 3.

Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats

Forest Ecology and Management (2014)

doi:10.1016/j.foreco.2014.11.003

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Abstract

Tropical forest regeneration is hindered by human-induced fires. After deforestation by fires, *Pteridium* spp. (bracken fern) often colonizes and dominates the vegetation for long time periods, presumably inhibiting the succession. Tree species from mature forests are rare in the degraded areas, potentially due to the lack of seed dispersal and unfavourable abiotic conditions. Here, we experimentally assess the effect of bracken presence, in terms of litter and shade, on seedling recruitment of three native, shade-tolerant tree species in the tropical mountains of Bolivia. In a spatially blocked design at eight sites, we compared seedling recruitment, survival and growth three months and one year after sowing between experimental litter and vegetation treatments and among habitat types (forest interior, degraded habitats close and far from the edge) and species (*Clusia sphaerocarpa*, *C. lechleri* and *C. trochiformis*). We found that species differed in their recruitment success and habitat preferences, but responded similarly to experimental treatments. Litter removal increased temperature and reduced humidity on the ground and vegetation removal increased canopy openness. Seedling recruitment was consistently reduced by litter and vegetation removal, and their interaction had a deleterious negative effect. Seedling survival and growth were also reduced by litter removal. Our results highlight the overlooked facilitative effects of bracken by ameliorating harsh abiotic conditions and increasing the probability of *Clusia* seedling recruitment and potentially other shade-tolerant tree species in degraded habitats. To enhance forest regeneration in fire-degraded areas, we recommend spreading seeds of shade-tolerant tree species into the bracken vegetation. This method is less costly and might be more efficient than previous methods that involved repeated bracken removal. Recruitment of late-successional species in the bracken vegetation is likely to promote the restoration of tropical forest; however, long-term studies are needed to test the success of such efforts.

Keywords: *Clusia*; facilitation; forest recovery; litter; montane forest; *Pteridium arachnoideum*.

Chapter 4.

Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics

Manuscript (under review)

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Abstract

Question: Is forest regeneration in tropical bracken-dominated habitats hindered by seed limitation and/or establishment limitation?

Location: Tropical montane forest and bracken degraded habitat in Bolivia.

Methods: We experimentally assessed the effect of bracken fronds on natural seedling recruitment in a tropical montane forest of the Bolivian Andes. At ten sites, we placed 240 m-long transects ranging from the forest interior to the degraded habitat and installed paired plots at seven distances along each transect. In one plot of each pair, we applied a repeated vegetation removal treatment to assess the effect of bracken on natural seedling recruitment. We analysed the effect of bracken removal on species richness, seedling survival and growth, and the effect of distance to the forest edge and vegetation removal on species richness of forest and non-forest species.

Results: Species richness was higher in the forest than in the degraded habitat. Forest species corresponded to approx. 60% of the species pool in the degraded habitat, but were present at low densities. Species richness of forest seedlings in the degraded habitat decreased with increasing distance from the forest edge, corroborating seed limitation. Forest species seedlings had high survival in the degraded habitat, especially under bracken fronds, suggesting a lack of establishment limitation. Vegetation removal in the degraded habitat did not affect species richness, but significantly reduced seedling survival and growth of forest species.

Synthesis: Our results emphasize that the lack of seed dispersal hinders natural regeneration of bracken-dominated habitats in the tropics and suggest that bracken fronds facilitate seedling establishment. We recommend seed addition of forest species into the bracken vegetation to accelerate the forest regeneration process.

Keywords: Bolivia; Establishment limitation; Facilitation; Forest restoration; Natural regeneration; *Pteridium arachnoideum*; Seed limitation; Seedling recruitment; Seedling survival; Species richness.

Chapter 5. Synthesis

General discussion

The aim of the thesis was to investigate the limiting factors on forest regeneration in bracken degraded habitats in a montane forest of Bolivia. I asked whether forest regeneration is hindered by seed limitation and/or establishment limitation. This study reveals that the main factor limiting forest regeneration in bracken degraded areas in the montane forest is seed limitation. Seedling establishment limitation, which is commonly found in disturbed areas, was not supported by the findings of this study. Seedling recruitment in the degraded areas was favoured along several steps of the life cycle: (i) secondary dispersal by ants increased seedling recruitment by increasing seed germination and reducing seed predation; (ii) seed predation in the degraded habitat was generally low; (iii) seedling emergence and recruitment of three shade-tolerant *Clusia* species was favoured in the presence of bracken vegetation and litter; and (iv) seedling recruitment of the community, including forest and non-forest species, responded positively to the presence of bracken vegetation. With this study I suggest that bracken does not represent an inhibiting species for the regeneration of the montane forest, as was previously suggested (e.g., Silva Matos & Belinato 2010; Miatto *et al.* 2011; Ribeiro *et al.* 2013), but it rather could facilitate seedling recruitment by ameliorating the harsh conditions in the open area. However, these results have to be considered with caution because this study only assesses the limitations during the seedling stage and long-term monitoring will be needed to confirm these findings.

Seed limitation

This study confirmed seed limitation as the main factor hindering forest regeneration in bracken-dominated areas. The lack of seed dispersal contributed to a decrease in species richness of forest seedlings with increasing distance from the forest edge (Chapter 4). Most studies in tropical disturbed areas found that lack of seed dispersal is the main limiting factor on forest recovery (reviewed by Holl 2002, 2012). Seed limitation in most tropical habitats is related to the large number of forest species that depend on animals for seed dispersal (Howe & Smallwood 1982). Forest disturbance particularly affects large-seeded animal-dispersed species, reducing plant-frugivore interactions and therefore seed dispersal into degraded habitats (Markl *et al.* 2012). The lack of perching structures, food resources and high predation risk in disturbed areas results in an avoidance of these areas by seed dispersers (Wunderle 1997). The short viability of most large, animal-dispersed seeds implies that these species are also absent from the soil seed bank (Benítez-Malvido, Martínez-Ramos & Ceccon 2001; Da Silva & Silva Matos 2006; Lippok *et al.* 2013b). Seed limitation is normally reflected in the seed rain, and numerous studies in disturbed habitats report that richness and abundance of animal-dispersed seeds rapidly decline with increasing distance from the forest edge (e.g., Aide & Cavelier 1994; Holl 1999; Dosch, Peterson & Haines 2007). The same pattern was found in a parallel investigation in my study area (F. Saavedra unpubl. data). Therefore, my results suggest that species richness of forest seedlings is consistent with seed rain patterns in this area.

However, despite seed limitation, I found that 60% of the seedling species pool in the bracken degraded habitat was constituted of forest-species (Chapter 4), but they only represented one third of the seedling individuals. The other two thirds were principally represented by bracken and wind-dispersed shrubs from the families Asteraceae and Fabaceae. These non-forest species are typically abundant in the soil seed bank and are easily dispersed by wind from surrounding degraded habitats (Dupuy & Chazdon 1998; Holl 1999; Zimmerman *et al.* 2000). Non-forest species were more dominant in a bracken degraded area in Ecuador; however, forest species were still absent after 48 months, possibly due to long distances to forest sources (Palomeque 2012). The small number of graminoids in my observations in the degraded habitat (8 % of the individuals) highlights the negative effect of bracken on grasses, confirming previous studies in other bracken degraded areas (e.g., Marrs & Watt 2006; Roos, Rödel & Beck 2010). This result highlights the importance of bracken on outcompeting grasses which are highly competitive against tree seedlings.

Seed limitation has also been related to high seed predation rates in disturbed habitats (Uhl 1987; Aide & Cavelier 1994; Holl & Lulow 1997). Based on vertebrate exclusion experiments to assess the main seed predator agents, the results of my study indicated that the main seed predators were vertebrates (Chapter 2). Small mammals, especially rodents, are widely recognized as seed predators, limiting seedling recruitment and abundance (e.g. Bricker, Pearson & Maron 2010). Seed predation in the bracken degraded habitat was relatively low (ranging from 20 to 30%). In comparison, 35-100% of the seeds were predated in an abandoned farm in the Amazon of Venezuela (Uhl 1987), 10-80% in a grassland in lowlands in Colombia (Aide & Cavelier 1994), and 63% in a montane pasture in Costa Rica (Holl & Lulow 1997). Interestingly, I found that secondary dispersal by ants reduced seed predation risk in the degraded habitats (Chapter 2), by rapidly reducing seed clustering and hiding seeds beneath the litter layer, which has been shown to be advantageous in previous studies (Turnbull & Culver 1983; Clark, Clark & Jacobi 1991; Hulme 1994).

Secondary dispersal by ants promoted seed germination and seedling recruitment in the degraded habitat by directed seed dispersal. Ants frequently dispersed the seeds beneath the litter layer, concurring with the suggestions of other authors (e.g., Pizo & Oliveira 1998). Directed seed dispersal was important because the harsh abiotic conditions in open habitats can be diminished beneath the litter layer (Facelli & Pickett 1991; Loydi *et al.* 2013). This effect was confirmed in Chapter 3, where microclimatic conditions in the degraded habitat beneath the litter layer favoured seed germination and seedling recruitment of *Clusia* species. Therefore, ants demonstrated to be effective seed dispersers by directing seeds beneath litter and reducing the risk of seed predation. If enough seeds were dispersed to the degraded habitats, ants could relocate them decreasing their probability of predation and increasing their probability of germination and seedling recruitment.

Establishment limitation

With my experiments, I could not detect an establishment limitation in bracken degraded habitats. This was reflected with litter and vegetation removal experiments at the population level (with *Clusia* species, Chapter 3) and with vegetation removal treatments at the community level (Chapter 4). Seed germination and seedling recruitment patterns at the population level for three shade-tolerant *Clusia* species were similar to those encountered at the community level. At the population level, the results show that bracken shade and especially litter have a positive effect on seedling recruitment, survival and growth of the three *Clusia* species. Litter presence ameliorated the harsh abiotic conditions in the ground surface by reducing maximum temperatures by 20°C and increasing relative humidity by 35% (Chapter 3). Previous studies demonstrated that litter increases seedling recruitment of other large-seeded, shade-tolerant species in disturbed areas (Facelli & Pickett 1991; Ganade & Brown 2002; Hölzel 2005; Loydi *et al.* 2013). This contrasts to the response of small-seeded, early-successional species that usually react negatively to litter presence (Facelli & Pickett 1991; Vázquez-Yanes & Orozco-Segovia 1993; Dalling & Hubbell 2002; Hölzel 2005; Loydi *et al.* 2013). It was not possible to assess the effect of litter on seedling recruitment at the community level (Chapter 4). This was due to the difficulty of finding, identifying, measuring and tracking the seedlings within the litter layer. However, I suggest that the positive effects of litter in bracken degraded areas are applicable to most large-seeded, shade-tolerant species. Large-seeded species usually require higher moisture than small-seeded species, and are adapted to germinate and recruit under litter (Leishman *et al.* 2000; Moles & Westoby 2004).

Vegetation removal in the bracken-dominated habitat reduced seedling recruitment and survival of the three *Clusia* species, mostly during the first three months. Vegetation removal increased irradiance and maximum temperatures, especially when litter was also removed. Previous studies revealed that direct irradiance increases soil temperatures above the ground and consequently soil evaporation, exposing seeds to dehydration (Vázquez-Yanes & Orozco-Segovia 1993). Desiccation sensitivity is common in late-successional, shade-tolerant tropical forest trees (Vázquez-Yanes & Orozco-Segovia 1984; Holmgren *et al.* 2012). Previous investigations in disturbed areas also revealed negative effects of vegetation removal on seedling recruitment of late-successional species, but found the opposite trend for early-successional species (e.g., Ganade & Brown 2002; Günter *et al.* 2009; but see Holl 1999). Since shade and litter provided by bracken facilitated seedling recruitment and survival of the three *Clusia* species, it is likely that bracken could also facilitate seedling recruitment of other late-successional tree species.

I found a positive effect of bracken vegetation on seedling survival at the community level (Chapter 4). This effect was consistent for forest and non-forest species.

Although a previous study in a bracken degraded area in Ecuador reported a positive effect of bracken fronds on species richness, these sites were dominated by non-forest species (Palomeque 2012). My study plots presented numerous forest species and their performance was also enhanced by bracken shade. Most forest species in my study (Chapter 4) corresponded to large-seeded and animal dispersed species, which are characteristic traits of shade-tolerant species (Leishman *et al.* 2000; Moles & Westoby 2004). Seedling survival of forest species was even higher than that of non-forest species in the degraded habitat. This pattern concurs with the characteristics of large-seeded forest species that generally have higher survival than small-seeded species (Leishman *et al.* 2000; Moles & Westoby 2004). Seedling survival of *Clusia* species after one year ranged from 30% when vegetation and litter were removed to up to 50 % when vegetation and litter were present. At the community level, seedling survival of forest species after two years ranged from 65% when vegetation was removed to up to 75% when vegetation was present. These estimates are much higher than those found in a meta-analysis of restoration of degraded ecosystems, where more than half of the reviewed studies reported seedling survival lower than 20% within the first two years (Gómez-Aparicio 2009). My results suggest that establishment limitation in the bracken degraded habitat is lower than in other disturbed ecosystems. This could be related to a less competitive behaviour of bracken compared to grasses.

The dominance of bracken over the first years after burning leads to relatively constant environmental conditions under its canopy over time, suggesting that the performance of the seedlings could be also maintained. Bracken offers abiotic conditions more similar to the forest than to an open degraded habitat (Chapter 3) or a pasture. Bracken potentially influences the surrounding vegetation by its fronds, litter, rhizomes and allelopathy. I showed that bracken fronds and litter have positive effects on recruiting seedlings. Below-ground interference by rhizomes have been previously revealed to be low (Den Ouden 2000). Although bracken allelopathy has been often proposed, most studies assessing its allelopathic effects found contradictory and species-specific results, suggesting that this effect is generally weak (Dolling 1996; Den Ouden 2000; Marrs & Watt 2006; Priewasser 2013). These findings suggest that the effect of bracken on forest species needs to be reevaluated especially in the context of restoration programs.

Conclusions and management recommendations

There is no doubt that forest regeneration in bracken-dominated areas within the tropics is slow. However, the high seedling survival and growth that forest species exhibited during the experiments at the population and community level argue against an establishment limitation on forest regeneration in bracken degraded areas. The present study reveals an overseen importance of bracken on seedling recruitment of forest species, due to an amelioration of the harsh abiotic conditions in degraded habitats. The study also highlights that seed limitation is the main limiting factor for forest regeneration, due to a lack of animal-mediated seed dispersal. The results of this study reveal the potential of late-successional species for reforestation practices in bracken-dominated habitats, due to their ability to recruit in the presence of bracken vegetation and litter. However, due to their ecology, it is expected that late-successional species will take a long time to grow, but would constitute a late-successional vegetation that can persist for long periods. Although this study was restricted to the seedling and sapling stages, I observed some young shade-tolerant trees that overgrew bracken close to my experimental plots.

To formulate management recommendations to restore the forest, it is important to consider the natural rate of recovery of the ecosystem that depends on i) the ecosystem resilience to disturbance, ii) the land-use history, and iii) the landscape context in the surrounding matrix (Holl & Aide 2011). First, the tropical montane forest in general, and our study area in particular, have low resilience, mainly due to seed limitation (Chapter 4). The low resilience is represented by the slow forest regeneration (e.g., Günter *et al.* 2007; Miatto *et al.* 2011; Ribeiro *et al.* 2013). Second, the land use history of these areas is characterized by frequent fires during decades. Therefore, forest succession has been continuously interrupted. Third, most of the surrounding areas correspond to bracken-dominated lands and pastures, both vegetation types being fire-prone. However, in our area, and in most parts of the montane forest, there are many forest patches with relatively well preserved vegetation that potentially will serve as seed sources. These three factors highlight the necessity of an active restoration approach to accelerate the recovery of the tropical montane forest in bracken degraded areas.

Although most previous studies recommended that shrubs or early-successional tree species might be planted before introducing late-successional species in disturbed areas (e.g., Gómez-Aparicio 2009; Douterlungne & Thomas 2013; Shoo & Catterall 2013), this study shows that the introduction of late-successional species directly into the bracken vegetation, without removing bracken fronds or litter, could be a better alternative. Seed addition of late-successional species has been shown to be a good method in other disturbed areas, but usually after vegetation removal, mainly due to competitive superiority of grasses (e.g., Camargo, Ferraz & Imakawa 2002; Bonilla-Moheno & Holl 2010; Cole *et al.* 2011). The costs could be reduced in comparison to those of frequent vegetation removal and transplantation of early-successional nursery raised seedlings, which are the common strategies in bracken-dominated areas in the tropical region (e.g., Günter *et al.* 2009; Silva Matos & Belinato 2010; Douterlungne & Thomas 2013; Shoo & Catterall 2013). Direct seed addition can be more cost-effective than outplanting and can be applicable to larger scales (Brooks, Cordell & Perry 2009; Cole *et al.* 2011). Additionally, the inclusion of arillate-seeds could increase their recruitment probability by directed seed dispersal by ants.

It is important to highlight that this mechanism applies to ecologically, but not necessarily economically important plant species. Most economically important plant species have fast-growing early-successional characteristics, which might not be facilitated by bracken litter and fronds. Seed addition would primarily help the recovery of late-successional species. The high germination rates and seedling survival of *Clusia* species, along with their shade-tolerant characteristics, demonstrate the high potential of this genus to be included in future restoration approaches. Other animal dispersed tree forest species that had good performance in our study, such as *Myrsine coriacea*, *Viburnum* spp. and *Vismia* spp. could also be included (see also appendix in Chapter 4). We show that manual seed addition is one approach to mimic seed dispersal. This strategy could be enhanced by the inclusion of perch structures to increase natural seed dispersal by birds (Holl 1998;

Graham & Page 2012; Reid & Holl 2013). Although the importance of perch structures may be low in disturbed areas with establishment limitation (Reid & Holl 2013), I did not observe establishment limitation in bracken-dominated areas. Therefore, perch structures could enhance seed dispersal and seedling establishment of large-seeded forest species. Previous studies have suggested active promotion of the formation of small reforested islands (>50 m^2) that are likely to connect in the future (Zahawi *et al.* 2013). This could be achieved by spreading seeds of shade-tolerant species in small patches and adding perches that could eventually help develop nuclei of reforestation. As frequent fires are the major threat hindering long-term restoration in these areas, fire outbreaks and the implementation of policies to reduce fire frequencies are essential to ensure the long-term success of these strategies.

My findings suggest that forest regeneration in bracken-degraded habitats is hindered by seed limitation, related to the scarcity of animal seed dispersal, and not by establishment limitation. They also highlight the necessity of seed addition of shade-tolerant species into the intact bracken vegetation. This approach would exploit the facilitative effects of bracken on shade-tolerant species. I conclude that bracken forms a fast-growing pioneer vegetation that could promote forest regeneration in many ecosystems after seed addition. However, long-term studies are needed to monitor the effectiveness of such forest restoration strategy.

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Acknowledgements

I would like to express my deepest gratitude to Prof. Isabell Hensen and Dr. Matthias Schleuning for the opportunity to work in the project. Isabell advised me and unconditionally supported me throughout the thesis. I am very grateful to Matthias for his dedicated guidance and supervision, for sharing his expertize with me and enhancing the quality of my research. I would like to express my greatest appreciation to Prof. Katrin Böhning-Gaese for her kind hospitality in the Biodiversity and Climate Research Centre (BiK-F) in Frankfurt am Main, giving me the opportunity to share the experiences with her working group and receiving me as a working group member. Dr. Stephan G. Beck is always an inspiration for my work.

I would also like to thank my project colleagues and friends Francisco Saavedra, Denis Lippok, Amira Apaza, Stephan Kambach and Florian Walters for all their support. The experiences and adventures that we shared are unforgettable.

I am very grateful to all my field assistants and friends Marcela Velasco, Rodrigo Velasco, Gisela Franco, Viviana Baltz, Jud Rojas, Andrea Antezana, Richard Villegas, Consuelo Campos, Luis Marconi, Eduardo Aguirre, Ulises Salinas and Américo Guzmán, for their unconditional help and fun experiences in the forest. I also would like to thank to the people from Chulumani for their cooperation and support.

The seedling identification process would not be possible without the patience and expertize of the staff from the Herbario Nacional de Bolivia (LPB). I am deeply indebted with Stephan Beck, Alfredo Fuentes, Serena Achá, Luis Marconi, Paola Pozo, Rosy de Michel, Denis Lippok, Carla Maldonado, Freddy Zenteno, Ivan Jimenez, Fabricio Miranda and Isabel Loza. I also thank Miguel Limachi and Omar Osco for ant and rodent identification and sharing their ecological knowledge with me, and to Sergio Colque and Silvia Gómez for their cooperation in the laboratory.
I appreciate the support of the Böhning-Gaese group, especially Diana Bowler, Baptiste Schmid, Mathias Templin, Claudia Grünewald, Eike Neuschulz, Matthias Dehling and Tanja Caprano. I am very thankful to Diana for reading and polishing the manuscripts. I would like to thank Diana, Matthias, Denis and Baptiste for having a final look at the thesis.

I thank all my friends from Chulumani, La Paz, Frankfurt and Halle for joining me in this journey.

Finally, I am deeply grateful to Edgar, Silvia, Paty, Fidelia, Ana María, Tania, Gisela, Sergio and all my family for their help, encouragement, inspiration and support.

I thank the German Research Foundation (DFG), Martin-Luther-Universität Halle-Wittenberg and Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz of Hesse's Ministry of Higher Education, Research, and the Arts (LOEWE) for financial support.

Appendix A

Curriculum Vitae

Personal information

Name: Silvia Cecilia Gallegos Ayala
Date of birth: 14.09.1981
Place of birth: La Paz, Bolivia
e-mail: silvia.gallegos.a@gmail.com

Education

2010- Ph.D. student at Martin-Luther Halle-Wittemberg University, Institute of Biology (Prof. Dr. I. Hensen), Halle, Germany / Biodiversity and Climate Research Centre (BiK-F), (Dr. M. Schleuning), Frankfurt am Main, Germany.
Topic: "*Factors limiting forest regeneration in bracken-dominated areas in the tropical montane forest of Bolivia*"

2009 Licentiate in Biology*. Universidad Mayor de San Andrés (UMSA), La Paz, Bolivia. (Dr. S.G. Beck) Defense score: 99%.
Thesis: "*Composition, diversity and structure of a Tucuman-Bolivian forest in the Bermejo upper river basin (Tarija, Bolivia)"*.

1999 High school graduate (Bachiller en Humanidades): Instituto Educativo "Los Pinos", La Paz, Bolivia.

* Licenciatura: equivalent to a Master degree.

Work experience

2009 Field and laboratory assistant in Diploma thesis "Revision and biogeographical analysis of the species-complex around *Asplenium serra* s.s. (Aspleniaceae)" Diploma-Student Rayko Jonas from Systematische Botanik, Albrecht von Haller Institut für Pflanzenwissenschaften – University of Göttingen

2008-2009 Editor of the chapter "Vegetation and floristic diversity" in the book: "Biodiversity in the Bermejo River Basin"

2008 Field technician in the 3th and 4th phases of "Identification of diversity, distribution, management and implementation of conservation actions for *Theobroma* and *Anacardium* species" in the project "In situ conservation of crop wild relatives through enhanced information management and field application" UNEP/GEF.

2007 Natural Science Teacher – Primary School level. Unidad Educativa Utasawa.

2005-2006 Assistant of Botany in the project "Biodiversity in the Bermejo River Basin". SG/OEA – FUND-ECO, PEA Bermejo – Instituto de Ecología, Herbario Nacional de Bolivia (LPB).

2004 Teaching assistant in Laboratory of Systematic Botany of Non Vascular plants (Dr. M. Franken), Universidad Mayor de San Andrés, La Paz, Bolivia.

2004 Research internship "Ecological conditions of six species of traditional use in the Yungas of La Paz, Bolivia", UMSA.

Publications of the dissertation

Gallegos, S.C., I. Hensen & M. Schleuning (2014) Secondary dispersal by ants promotes forest regeneration after deforestation. *Journal of Ecology*, **102**, 659-666.

Gallegos, S.C., I. Hensen, F. Saavedra & M. Schleuning (2014). Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats. *Forest Ecology and Management.* doi: 10.1016/j.foreco.2014.11.003

Gallegos, S.C., S.G. Beck, I. Hensen, D. Lippok & M. Schleuning (Manuscript) Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics (*under review*)

Additional publications

Lippok, D., S.G. Beck, D. Renison, **S.C. Gallegos**, F.V. Saavedra, I. Hensen & M. Schleuning (2013) Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management*, **295**: 69–76.

Contribution to conferences

Gallegos, S.C., I. Hensen & M. Schleuning (2013) Secondary dispersal by ants enhances seedling recruitment in a fire-degraded tropical montane forest. *Annual Meeting of the Society of Tropical Ecology (GTÖ)*, Vienna, Austria. Oral presentation.

Gallegos, S.C., I. Hensen & M. Schleuning (2011) Recruitment of *Clusia lechleri* as a model species on the regeneration of a tropical montane forest in Bolivia. *3rd Bolivian Congress of Ecology*, Chuquisaca, Bolivia. Poster presentation.

Appendix B

Erklärung über den persöhnlichen Anteil an den Publikationen

Study 1 (Chapter 2):

Silvia C. Gallegos, Isabell Hensen & Matthias Schleuning (2014). Secondary dispersal by ants promotes forest regeneration after deforestation. *Journal of Ecology* 102, 659–666.

Design and data collection: **Silvia C. Gallegos** (90%), Matthias Schleuning (10%)
Data analysis: **Silvia C. Gallegos** (70%), Matthias Schleuning (30%)
Writing: **Silvia C. Gallegos** (70%), Matthias Schleuning (25%), Isabell Hensen (5%)

Study 2 (Chapter 3):

Silvia C. Gallegos, Isabell Hensen, Francisco Saavedra & Matthias Schleuning (2014). Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats. *Forest Ecology and Management.* doi: 10.1016/j.foreco.2014.11.003

Design and data collection: **Silvia C. Gallegos** (85%), Matthias Schleuning (10%) Francisco Saavedra (5%)
Data analysis: **Silvia C. Gallegos** (70%), Matthias Schleuning (30%)
Writing: **Silvia C. Gallegos** (65%), Matthias Schleuning (20%), Isabell Hensen (10%), Francisco Saavedra (5%)

Study 3 (Chapter 4):

Silvia C. Gallegos, Stephan G. Beck, Isabell Hensen, Denis Lippok & Matthias Schleuning. Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics (*manuscript under review*)

Design and data collection: **Silvia C. Gallegos** (75%), Stephan G. Beck (15%), Matthias Schleuning (10%)
Data analysis: **Silvia C. Gallegos** (70%), Matthias Schleuning (25%), Stephan G. Beck (5%)
Writing: **Silvia C. Gallegos** (65%), Matthias Schleuning (25%), Denis Lippok (5%), Isabell Hensen (5%)

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel “**Factors limiting forest regeneration in bracken-dominated areas in the tropical montane forest of Bolivia**” bisher weder der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale),
Unterschrift: ______________________________________ (Silvia C. Gallegos)