Seed dispersal by birds in tropical montane forests: towards a functional understanding of seed-dispersal effectiveness after deforestation

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Cover photo

Andean guan (*Penelope montagnii*) perching on a fruiting tree of *Solanum sp.* (Photo by Avalos V.)

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Summary

Tropical montane forests in the Andes harbor a high diversity of fleshy-fruited plant and frugivorous bird species, being one of the most diverse ecosystems in the world, but at the same time less understood in their community and ecosystem dynamics. Seed dispersal in tropical ecosystems is particularly animal-dependent where up to 90% of woody plant species produce fleshy fruits that are dispersed by frugivorous animals. Therefore, seed dispersal plays a pivotal role in maintaining and recovering the structure, diversity and functionality of tropical ecosystems. The study of the functional role of seed disperser assemblage in mutualistic networks links species interactions with ecosystem functioning and may determine the quantitative and qualitative components of seed dispersal effectiveness (SDE) at community level. Several studies in tropical ecosystems have shown that seed dispersal effectiveness may be modified by human land-use activities, such as deforestation. Consequently, human deforestation resulted in the creation of vast areas of forest edges and deforested habitats. Given their ubiquity, it is important to study the effects of human-induced forest edges on ecological processes, such as seed dispersal, in order to investigate its role on ecosystem functioning, plant demography and potential contribution to the regeneration of deforested habitats.

Since little is known about the effects of human-induced forest edges on SDE in tropical montane forests, this thesis aims to investigate the effect of forest edges on quantitative (*i.e.,* number of visits and number of seeds dispersed per visit) and qualitative (*i.e.,* seed deposition pattern) components of SDE by analyzing functional traits as the mechanism behind the effectiveness of seed dispersal. I asked how the functional diversity of avian seed dispersers in seed dispersal networks influences quantitative and qualitative components of SDE in human-disturbed tropical forests. This is the first attempt to integrate functional diversity and seed dispersal networks with the SDE framework at community level. As model species, I studied three *Clusia* species showing an ornithocorous seed dispersal syndrome: *Clusia sphaerocarpa, Clusia lechleri* and *Clusia trochiformis*. These species are typical components of plant communities in tropical montane forest, are among the most important food resources for frugivorous birds and are easy to identify throughout all recruitment stages in the field.

The thesis comprises three studies. In the *first study* I analyzed the frugivore community and seed dispersal and tested whether relationships between morphological bird traits (*i.e.,* body mass, gape width and wing tip length) and functional roles of seed dispersers' drive seed dispersal effectiveness in response to human-induced forest edges. Forest edges had a positive effect on the abundance and richness of frugivorous birds. Fruit removal rate was higher at forest edges, and seeds were less clustered dispersed at forest edges than in the interior. The functional and interaction diversity of the seed dispersal networks were higher at edges than in the interior, but functional and interaction evenness did not differ. The interaction strength of bird species was positively associated with morphological bird traits in the forest interior, but was not related to bird morphologies at forest edges. The high structural and functional diversity of networks at forest edges led to enhanced quantity and tentatively enhanced quality of seed dispersal.

In the *second study*, I tested the relationship between the quality of seed deposition and seedling recruitment patterns of three sympatric species of *Clusia* and tested whether this relationship changes between habitat types and different recruitment stages. The seed deposition pattern was similar between habitat types and probably driven by the high number of null dispersal events and delimited foraging movements of their main seed dispersers. The abundance of *Clusia* seedlings was higher at forest edges than in the forest interior. The spatial distribution of individuals changed among recruitment stages. While seedlings were randomly distributed, saplings and adult trees were more clustered than expected from a random distribution. The initial seed-deposition pattern generated by frugivorous animals was, thus, largely disconnected from the ultimate plant recruitment patterns, which has important implications for population growth and plant community dynamics at forest edges.

In the *third study*, I assessed the relationship between the quality of seed rain and seed traits patterns along habitat types (*i.e.,* forest interior vs. forest edge vs. deforested habitat) and tested the effect of perch structures on the dispersal of avian dispersed plant species toward deforested habitats. The seed abundance and species richness of fleshy-fruited plant species decreased strongly from the forest edge

toward deforested habitats. Perch structures increased the dispersal of seeds into deforested habitats. Seed mass, length and width decreased from the forest interior to deforested habitats. The reduction in the diversity and abundance of large-seeded and late-successional seed species dispersed from the forest interior to deforested habitats suggests a strong functional seed trait limitation toward deforested habitat. The presence of perch structures in these habitats may be the initial step for the amelioration of seed dispersal limitation in disturbed habitats.

In conclusion, most of the studies in human-induced forest edges have documented that seed dispersal effectiveness is disrupted by reducing the quantity and quality of seed dispersal. However, here I demonstrated that quantitative components such as the number of visits and number of seeds dispersed per visit were enhanced at forest edges, while qualitative components, such as the seed deposition pattern that was less clustered at forest edges, deserve more analysis in future studies. The high structural and functional diversity of seed dispersal networks at forest edges suggests that these seed dispersal networks are more robust against disruption than those in the forest interior because of functional redundancy of seed dispersers. Consequently, effects of human disturbance may alter the relationship between functional traits and functional importance of frugivore species in seed dispersal networks and lead to a more even contribution of different bird morphologies to seed dispersal at forest edges, which potentially could increase the effectiveness of seed dispersers and stabilize seed-dispersal functions in edge habitats. The increasing importance of small-bodied frugivore species in seed-dispersal networks at forest edges corroborates the findings that large-seeded and late-successional plant species were only rarely dispersed under perch structures in deforested areas. Changes in the functional structure of seed-dispersal networks, thus, can directly translate into changes in the functional structure of the dispersed seed communities in deforested habitats. Human assisted recovery of deforested habitats should aim to increase the number of mid- and long-distance seed dispersal events, in order to promote the dispersal of seeds by frugivorous birds into deforested habitats. The strong seed dispersal limitation of large-seeded and late-successional plant species in deforested habitats could be mitigated by the presence of perching structures. Thus, perches such as living shrubs and small trees may increase the number of seed

dispersal events toward deforested areas by attracting large-avian seed dispersers and promoting a regeneration process over time. Therefore, my findings help to increase our comprehension about the factors driving seed dispersal effectiveness at human-induced forest edges and adjacent deforested habitats. Thus, the development of new restoration strategies in deforested ecosystems should be addressed from a functional perspective of applied ecology.

Zusammenfassung

Die tropischen Bergwälder der Anden beherbergen eine große Vielfalt an Pflanzen mit fleischigen Früchten und frugivoren Vögeln. Sie sind weltweit eines der artenreichsten Ökosysteme, jedoch ist nur wenig über ihre Dynamik bekannt. Die Samenausbreitung in tropischen Ökosystemen beruht besonders auf Tieren und bis zu 90% der Gehölzarten produziert fleischige Früchte, die von frugivoren Tieren ausgebreitet werden. Daher spielt die Samenausbreitung für dem Erhalt und der Wiederherstellung der Struktur, der Artenvielfalt und der Funktionalität tropischer Ökosysteme eine entscheidende Rolle. Studien über die funktionelle Rolle der Samenausbreiter in mutualistischen Netzwerken verbinden die Wechselwirkungen zwischen den Arten mit Ökosystemfunktionen und können die quantitativen und qualitativen Bestandteile der Samenausbreitungseffizienz (SDE) ermitteln. Verschiedene Studien in tropischen Ökosystemen haben gezeigt, dass die SDE durch verschiedene Landnutzungsarten, wie z.B. Abholzung, beeinflusst wird. Großflächige Entwaldung resultiert in der Entstehung von Waldrändern und Offenflächen. Es ist wichtig die Effekte dieser anthropogen erschaffenen Waldränder auf die ökologischen Prozesse, wie z.B. Samenausbreitzung, zu untersuchen, um deren Effekte auf die Ökosystemfunktionen, Pflanzen-Demographie und einen möglichen Beitrag auf die Regeneration der Offenflächen beurteilen zu können.

Da nur wenig über die Effekte von anthropogenen Waldrändern auf die SDE in tropischen Bergwäldern bekannt ist, befasst sich diese Doktorarbeit mit den Effekten von Waldrändern auf quantitative (Anzahl der Besuche und Anzahl der ausgebreiteten Samen pro Besuch) und qualitative (Muster in der Samenausbreitung) Komponenten der SDA durch die Analyse der funktionellen Merkmale. Ich untersuchte wie die funktionelle Vielfalt der samenausbreitenden Vögel in Interaktionsnetzwerken die quantitativen und qualitativen Komponenten der SDE in gestörten tropischen Wäldern beeinflusst. Dies ist der erste Versuch, funktionelle Vielfalt und Interaktionsnetzwerke in das SDE-System auf Gemeinschaftsebene zu integrieren. As Modelarten benutzte ich drei vogelausgebreitete Arten der Gattung *Clusia*: *Clusia sphaerocarpa, C. lechleri* and *C. trochiformis*. Diese Arten sind typisch für die Pflanzengesellschaften tropischer Bergwälder, sie sind wichtige Nahrungsquellen für frugivore Vögel und sie sind leicht im Feld zu bestimmen.

Die Doktorarbeit besteht aus drei Untersuchungen. In der *ersten Studie* analysierte ich die Frugivoren-Gemeinschaft sowie die Samenausbreitung und testete, ob der Zusammenhang zwischen morphologischen Merkmalen der Vögel (Masse, Schnabelbreite und Flügelspannweite) und deren ökologische Funktion die SDE in Abhängigkeit von anthropogenen Waldrändern beeinflusst. Waldränder hatten positive Effekte auf die Häufigkeit und die Artenvielfalt der frugivoren Vögel. An Waldrändern wurden mehr Früchte entfernt und die Samenausbreitung war weniger gebündelt verglichen mit dem Waldesinneren. Die funktionellen Merkmale und die Interaktionen innerhalb der Netzwerke waren an Rändern vielfältiger als im Inneren, jedoch wurden keine Unterschiede in deren Gleichheit gefunden. Die Stärke der Interaktionen war im Waldesinneren positive assoziiert mit den morphologischen Merkmalen der Vögel, jedoch nicht am Waldrand. Die hohe strukturelle und funktionelle Vielfalt der Interaktionsnetzwerke an Waldrändern führte zu einer quantitativ und eventuell auch qualitativ verbesserten Samenausbreitung.

In der zweiten Studie untersuchte ich den Zusammenhang zwischen Samenausbreitung und Mustern in der Keimlingsetablierung dreier sympatrischer Arten der Gattung *Clusia*, und testete ob dieser Zusammenhang sich zwischen verschiedenen Habitaten und Regenerations-Phasen unterscheidet. Die Muster in der Samenausbreitung unterschieden sich nicht zwischen den Habitaten, was womöglich an einer großen Anzahl an Nicht-Ausbreitungs-Ereignissen und einer geringen Reichweite der wichtigsten Samenausbreiter lag. Die *Clusia*-Keimlinge kamen häufiger an den Waldrändern als im Waldesinneren vor. Die räumliche Verteilung der Individuen unterschied sich zwischen den Regenerations-Phasen. Im Gegensatz zu den Keimlingen welche zufällig verteilt waren, waren Schösslinge und die ausgewachsenen Bäume gebündelt. Die Muster der Pflanzen-Regeneration waren größtenteils unabhängig von den Mustern in der Samenausbreitung, was große Bedeutung für das Populationswachstum und die Dynamik der Pflanzengesellschaften an Waldrändern hat.

In der *dritten Studie* untersuchte ich den Zusammenhang zwischen der Qualität des Sameneintrages und der Samenmerkmalen in verschiedenen Habitaten (Waldinneres, Waldrand und Offenflächen) und testete die Effekte von Sitzplätzen auf den Sameneintrag durch Vögel in den Offenflächen. Die Menge und die Artenvielfalt von Pflanzen mit fleischigen Früchten nahm vom Waldrand in die Offenflächen hinein ab. Sitzplätze erhöhten den Sameneintrag in den Offenflächen. Die Masse, Länge und Breite der Samen nahm vom Waldesinneren zu den Offenflächen ab. Die starke Abnahme in der Samen-Vielfalt und Menge von Arten, welche große Samen haben und typisch für späte Sukzessionsstadien sind, deutet auf eine starke Limitierung bestimmter funktioneller Merkmale in den Offenflächen hin. Sitzplätze könnten den Sameneintrag in diesen Habitaten verbessern.

Die meisten Untersuchungen über die Effekte von anthropogen erschaffenen Waldrändern haben gezeigt, dass die SDE durch verminderte quantitative und qualitative Samenausbreitung verändert ist. Im Gegensatz dazu habe ich mit meinen Untersuchungen gezeigt, dass quantitative Bestandteile, wie z.B. die Anzahl der Besucher und die Anzahl an ausgebreiteten Samen je Besuch, an Waldrändern verbessert waren. Den qualitative Bestandteilen, wie den räumlichen Mustern der Samenausbreitung, die weniger geklumpt an Waldrändern waren, sollte in zukünftigen Studien mehr Beachtung geschenkt werden. Die hohe strukturelle und funktionelle Vielfalt der Interaktionsnetzwerke an Waldrändern deutet auf eine geringere Störungsanfälligkeit hin, welche auf funktioneller Redundanz der Samenausbreiter beruht. Anthropogene Störung könnte den Zusammenhang zwischen funktionellen Merkmalen und der Bedeutung der frugivoren Arten in den Interaktionsnetzwerken verändern und zu einer Angleichung der Bedeutungen der verschiedenen Vogelmorphen für die Samenausbreitung führen, was wiederum die Effektivität der Samenausbreiter und die Stabilität der Samenausbreitungsfuntion an Waldrändern erhöhen könnte. Die erhöhte Bedeutung kleinerer Arten in den Interaktionsnetzwerken an Waldrändern unterstützt das Ergebnis, dass großsamige Pflanzenarten später Sukzessionsstadien nur sehr selten unter die Sitzflächen in den Offenflächen ausgebreitet wurden. Veränderungen in der funktionellen Struktur von Ausbreitungsnetzwerken können also direkten Einfluss auf die funktionelle Struktur der ausgebreiteten Samengemeinschaften in den benachbarten Offenflächen haben. Um die Wiederherstellung der entwaldeten Offenflächen zu unterstützen, sollte die Mittel- und Langstrecken-Ausbreitung unterstützt und damit der Sameineintrag durch frugivore Vögel erhöht werden. Die starke Limitierung der großsamigen Arten der späten Sukzessionsstadien könnte durch die Anbringung von Sitzplätzen vermindert werden. Sitzplätze, wie Sträucher und kleine Bäume könnten durch Anlocken von größeren Vögeln die Ausbreitungsereignisse vermehren und somit den Regenerationsprozess unterstützen. Meine Ergebnisse helfen daher die entscheidenden Faktoren des SDE an anthropogen geschaffenen Waldrändern und naheliegenden Offenflächen besser zu verstehen. Neue Regenerierungs-Strategien für entwaldete Ökosysteme sollten daher unter dem Blickwinken der angewandten Ökologien erarbeitet werden.

Chapter 1 – General introduction

Andean montane forests are one of the most diverse ecosystems in the world, but at the same time one of the most threatened by deforestation and deliberate fires (Myers et al. 2000, Kessler & Beck 2001, Gerold et al. 2008). Montane forest habitats are modified and destroyed 30% faster than lowland tropical forests (O'Dea & Whittaker 2007). The rapid increase in human land-use activities resulted in the creation of vast areas of forest edges and deforested habitats (Hagen et al. 2012). Nowadays, human-induced forest edges constitute one of the most common disturbed habitats in the tropics (Tabarelli et al. 2008, Laurance et al. 2011) and given their ubiquity, it is important to study how human-induced forest edges modify the functional diversity of seed dispersers in seed dispersal networks and consequently how this translates into changes in the quantity and quality of seed dispersal in human disturbed habitats.

Seed dispersal effectiveness (SDE)

Seed dispersal is considered the demographic bridge linking the end of the reproductive cycle of adult plants with the establishment of their offspring (Jordano & Herrera 1995, Nathan & Muller-Landau 2000, Wang & Smith 2002, Schupp et al. 2010). Furthermore, seed dispersal by frugivorous vertebrates is the most common ecological process to maintain the structure, diversity and functionality of plant communities in tropical ecosystems (Howe & Smallwood 1982, Nathan & Muller-Landau 2000). Thus, frugivorous animals such as birds and mammals are the most important vectors to disperse seeds of fleshy-fruited plant species at specific locations in the environment (Jordano et al. 2011, Karubian et al. 2012), establishing the spatial template for subsequent ecological processes (Wang & Smith 2002, Jordano et al. 2011).

Understanding the consequences of seed dispersal by frugivorous birds on plant fitness it is a central question of plant community ecology and has long been recognized as a key ecological process in the tropics (Alcántara et al. 2000, Jordano 2000). However, not all seed dispersers provide equal benefits to fleshy-fruited plant species that are dispersed by a diverse assemblage of seed dispersers. Therefore, seed dispersers may differ in their effective contribution to the establishment of new individuals in the environment and consequently on plants demography (Spiegel & Nathan 2007, Calviño-Cancela & Martín-Herrero 2009, Carlo & Tewksbury 2014). In order to quantify the benefits of seed dispersal by frugivorous birds, the SDE framework helps to measure the contribution of an individual seed disperser to a particular plant species (at population level, Schupp 1993, Sun et al. 1997, Rodríguez-Pérez & Traveset 2010, Montaño-Centellas 2012), but it can also encompass and refer to the overall effectiveness of seed dispersal that a plant receives from an assemblage of seed dispersers (at community level, Schupp et al. 2010). Even though this is a central concept in seed dispersal ecology, few studies estimate SDE from a community perspective in disturbed ecosystems.

The SDE framework has been assessed in terms of the number of seeds dispersed by each seed disperser (*i.e.*, quantitative component) and the probability that a viable dispersed seed generates a new individual (*i.e.*, qualitative component) (Schupp 1993, Schupp et al. 2010). The quantity of seeds dispersed by frugivorous animals is determined by (1) the number of visits made by each seed disperser to fruiting plants and (2) the number of seeds dispersed per visit. Frugivorous animals and fleshy-fruited plants interact in complex mutualistic networks, wherein some species make frequent visits to several plant species, while other frugivores only visit few specific plant species. Likewise some species consume and disperse many seeds per visit, while others disperse only few seeds (Bascompte et al. 2003). Thus, the structure of mutualistic networks is described with the frequency of interactions that describes the strength of the interaction between species and the quantitative importance of particular species within networks (Bascompte & Jordano 2007).

The quality of seed dispersal is determined by (1) the quality of treatment in the mouth and gut of seed dispersers and (2) the quality of the seed deposition pattern in the environment (Schupp et al. 2010). The handling of fruits is associated to the feeding behaviour of the seed dispersers and the main benefits of gut treatment may affect the proportion of seeds that geminate after seed dispersal (Sun et al. 1997). In this thesis, I focus on the quality of seed dispersal in terms of the seed deposition patterns that influences the probability that a dispersed seed could reach a suitable site where a new individual could establish successfully as an adult tree (Pizo & Simao 2001). The main question in the quality of seed deposition is where the seeds are delivered, in particular the distribution of seeds relative to parent trees (*i.e.,* the seed shadow pattern) and from the seed source habitat (*i.e.,* the seed rain pattern).

Although SDE was broadly studied in different ecosystems and seed dispersal vectors (Graham et al. 1995, Jordano & Schupp 2000, Rodríguez-Pérez et al. 2010), few studies have analysed the SDE framework from a community perspective (but see González-Castro et al. 2014) and even less from a functional perspective. Therefore, differences in species interactions due to morphological traits (Bascompte & Jordano 2007) may be associated with the quantitative and qualitative importance of seed dispersers in seed dispersal networks (Schupp et al. 2010) and provide a better understanding of ecosystem functioning (Mouchet et al. 2010, Cadotte et al. 2011).

Functional diversity and SDE

Studies of frugivory by animals have recently started to incorporate functional traits of frugivorous animals to analyze the ecosystem function of seed dispersal (Moran et al. 2004, McGill et al. 2006). One possibility to extend studies of SDE to a functional perspective is provided by exploring the relationship of functional traits of interacting species in seed dispersal networks with quantitative and qualitative components of SDE. From a functional perspective, species can be described as an assemblage of traits that determine their functional role as well as their interactions with other species (McGill et al. 2006, Mouchet et al. 2010). Furthermore, functional traits are relevant to identify keystone species with particular importance in ecological communities, e.g. in terms of their contribution to the establishment of new plant individuals (Chapin et al. 1997). The functional diversity (FD) within a community (Díaz & Cabido 2001) can be measured in terms of the functional richness (FRic) of traits, which is defined as the size of the convex hull around the functional trait space and the functional evenness (FEve) described as the uniformity of the distribution of species abundances in the functional trait space (Mason et al. 2005, Villéger et al. 2008). The functional diversity of bird assemblages may affect the quantity (by enhancing the number of seeds dispersed per visit) and the quality (by distributing seeds to several habitat types) of seed dispersal (Jordano et al. 2007). Seed deposition patterns generated by an assemblage of seed dispersers with a high functional diversity could also have strong effects on the diversity of functional seed traits dispersed by frugivorous birds (Galetti et al. 2011) and thus on the composition of seed traits in the seed bank of regenerating habitats (Lippok et al. 2013b, Helsen et al. 2012). Changes in the functional structure of frugivorous bird communities (Neuschulz et al. 2012, Saavedra et al. 2014) could lead to an uneven distribution of seed traits in disturbed ecosystems (Costa et al. 2012). For instance, previous studies have shown that small-seeded tree species are more frequently dispersed in disturbed habitats than large-seeded tree species (Markl et al. 2012, Menke et al. 2012). Furthermore, changes in the size of seeds deposited in deforested areas may be associated to the homogenization of functional seed traits and the establishment of only a fraction of specific plant species.

Effects of human-induced forest edges on SDE

Ecosystem functions such as seed dispersal by frugivorous birds have been disrupted at human-induced forest edges by reducing the effectiveness of seed dispersal in terms of quantity and quality of dispersed seeds (Babweteera & Brown 2009, Schupp et al. 2010, Wotton & Kelly 2011). Nevertheless, recent studies have found that human-induced forest edges in tropical montane forests could have positive effects on avian seed dispersal, driven by the production of large crop sizes in fleshy-fruited plant species (Alberti & Morellato 2010) and corresponding increases in the abundance and richness of frugivorous bird species (Schleuning et al. 2011, Menke et al. 2012). In deforested and burned habitats, regeneration of tree species may depend upon continuous dispersal of seeds because other sources of regeneration are mostly lacking (Nepstad et al. 1996, Slocum & Horvitz 2000, McGill et al. 2006).

Most of the studies of forest regeneration have highlighted the importance of seed deposition patterns in the regeneration process of deforested areas by animal-dispersed plant species. Seed dispersal limitation, defined as the lack of seeds transported into deforested areas (*i.e.,* diminished quantity and quality of seed dispersal), is triggered by few mid- and large-distance seed dispersal events of fleshy-fruited plant species into disturbed habitats (Wotton & Kelly 2011) or by degraded seed source habitats (Oliveira et al. 2004, Santos et al. 2008). Seed dispersal limitation could be mitigated by the presence of remnant trees or the use of perching structures that could act as foci for the regeneration of plant communities (Galindo-González et al. 2000, Carrière et al. 2002, Hooper et al. 2005). The continuous dispersal of seeds by avian seed dispersers is crucial for the regeneration of deforested habitats (Carrière et al. 2002, Dosch et al. 2007). Thus, perching structures could enhance the probability that forest seed species reach deforested habitats by attracting avian seed dispersers (Holl 1998, Zanini & Ganade 2005, Heelemann et al. 2012).

Recent studies have started to explore how seed dispersal functions change along human disturbed habitats (Schleuning et al. 2011, Menke et al. 2012, Plein et al. 2013). Nevertheless, the knowledge of the impacts of human-modified habitats on avian-seed dispersal processes is still limited (Hagen et al. 2012). Understanding the consequences of seed dispersal by frugivorous birds for plant fitness is a central question for the regeneration of plant communities and has long been recognized as a key ecological process in the tropics (Alcántara et al. 2000, Jordano 2000). However, in spite of the growing body of studies integrating seed dispersal processes and functional diversity (Menke et al. 2012, Dehling et al. 2014, Saavedra et al. 2014), my study is among the first to examine the influence of habitat type on the relationship between the functional diversity of avian seed dispersers, seed dispersal networks and seed dispersal effectiveness in tropical montane ecosystems.

Study aims and objectives

This thesis aims to investigate the SDE framework by assessing the functional importance of seed dispersers in avian-seed dispersal networks in human-disturbed montane forests in the Bolivian Andes. Thus, I related morphological bird traits with quantitative (*i.e.,* the number of visits and the number of seeds dispersed per visit) and seed traits with qualitative (*i.e.,* seed deposition pattern) subcomponents of SDE. This is one of the first attempts to integrate functional diversity and seed dispersal networks with the SDE framework at community level. The thesis comprises three studies. The first one investigates the functional importance of seed dispersers in seed-dispersal networks and their influence on the quantity and quality of SDE and the two other studies analyze the quality of seed deposition patterns generated by frugivorous birds at population and community level. Since all studies incorporate the effect of human-induced forest edges on the relationship between species traits and the SDE framework, the results reveal predictions on the effects of human disturbance on the ecosystem function of seed dispersal by frugivorous birds.

In the first study (**Chapter 2**), I investigate the consequences of human-induced forest edges on the functional diversity of frugivorous birds and on the structure of seed dispersal networks. I investigated how frugivore communities and seed dispersal change between forest interior and forest edge. This study tested whether the relationship between bird traits and functional roles of species in the network influence quantitative and qualitative components of SDE. I recorded interaction frequencies between fleshy-fruited plant and frugivorous bird species and functional bird traits (*i.e.,* body mass, gape width and wing tip length). I found that an even importance of seed dispersers in seed dispersal networks at forest edges increased quantitative components of seed dispersal and generated a less clustered seed deposition pattern. Our results highlight the importance of functional and interaction diversity in seed dispersal networks. The even distribution of the strength of species interactions across bird morphologies at forest edges, thus, influences SDE. It also suggests that the effects of species traits on ecosystem functions can vary along small-scale gradients of human disturbance.

In the second study (**Chapter 3**), I investigated the relationship between seed deposition and spatial recruitment patterns. I tested whether spatial patterns of seeds and recruits change between habitat types and different recruitment stages of three sympatric *Clusia* tree species. I recorded the number of seeds deposited in a system of 20 seed traps and the density and distribution of recruits in plots of 20 x 100 m to evaluate seed deposition and recruitment patterns. I found that seed dispersal was higher at forest edges and more seeds were deposited by frugivorous birds close to parental trees in both habitats. The abundance and spatial distribution of recruits changed between habitat types and among recruitment stages. While seedlings were more abundant and randomly distributed, saplings and adult trees were less abundant and more clustered than expected from a random distribution. The delimited foraging movements of the main seed dispersers are likely to generate the clustered spatial pattern of seed deposition. In contrast, differences in spatial recruitment patterns between recruitment stages suggest impacts of environmental filters, such as light and water availability, which modify the initial seed-deposition pattern in later recruitment stages.

In the third study (Chapter 4), I analyzed the consequences of deforestation on the spatial distribution of seeds dispersed by frugivorous birds. I investigated differences in seed abundance, seed species richness and seed traits (*i.e.,* seed mass, seed length and seed width) of animal-dispersed plant species across different habitat types (*i.e.,* forest interior vs. forest edge vs. deforested habitat). I also tested the effect of artificial perch structures on the dispersal of seeds toward deforested areas. The seed rain pattern was recorded in a system of 38 seed traps installed along a transect of 250 m from the forest interior towards deforested areas. In deforested areas half of the seed traps were installed under perch structures. Functional seed traits and species origin (*i.e.,* late-successional, pioneer, non-forest species) were registered for all seed species. I found that the abundance and species richness of dispersed seeds decreased strongly from the forest edge towards deforested areas, especially for large-seeded late-successional species. In deforested areas, perch structures increased the abundance and to some extent the species richness, but did not alter the composition of seed traits and species origin. Differences in the seed deposition pattern resulted in a functional trait limitation of large-seeded and late-successional plant species in deforested habitats. The presence of perch structures may be a key initial step for the reforestation of these areas.

Study system

I conducted this study in the Bolivian “Yungas“ situated on the Eastern slope of the Andes at 16°10`southern latitude(Killeen et al. 2005, Navarro & Maldonado 2002). Our study area is located in the province Sud Yungas in the vicinity of the **Chulumani** town (1700 to 2200 m a.s.l., 16° 24′ 37.10” S. 67° 31’ 37.08” W)(**Figure 1**). The natural vegetation at this altitudinal belt can be classified as high-montane and montane forest (Killeen et al. 2005). The climate is seasonal with a short dry season from May to September and a wet season from November to April, when most of trees bear fruit. The mean annual precipitation is 2300 mm and the mean annual temperature is 16.8 °C (Schawe et al. 2010).

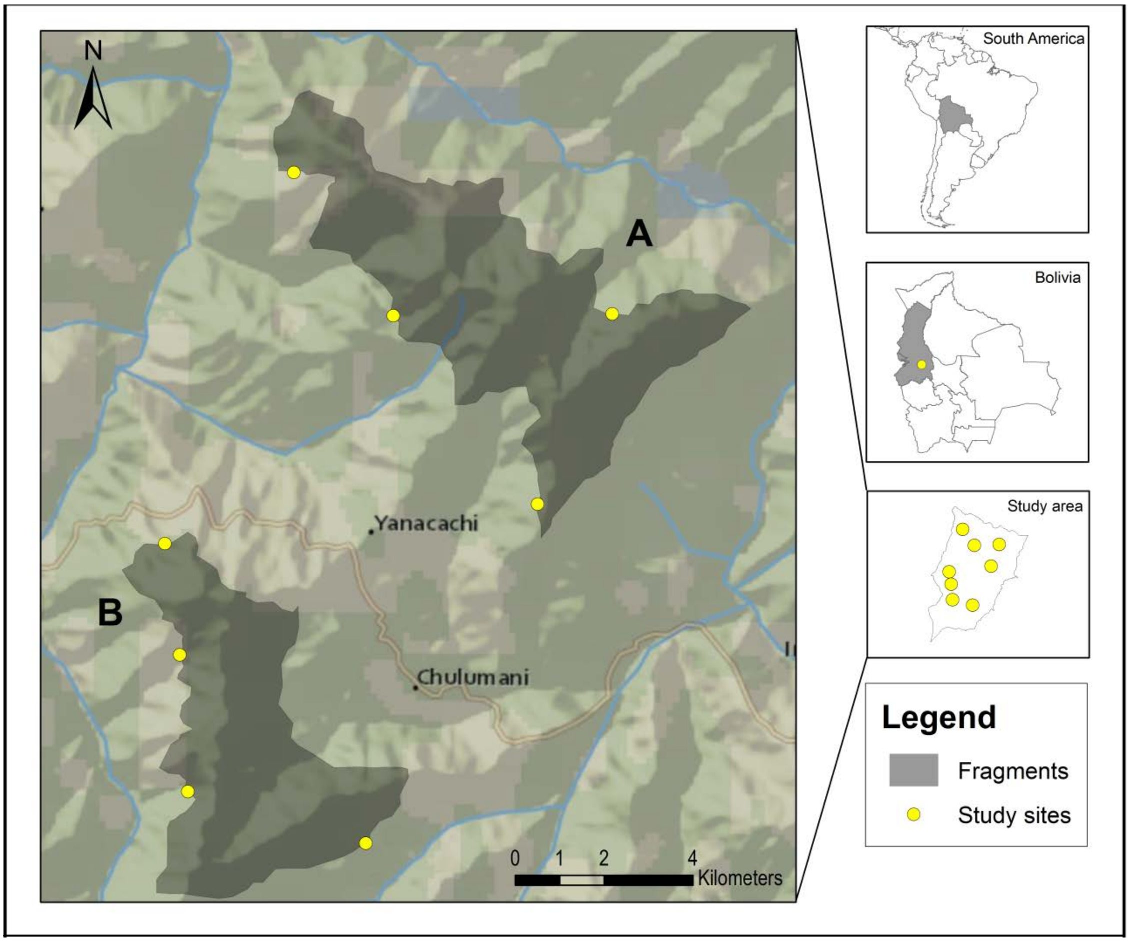

Figure 1. Map of the study area. Forest remnants are highlighted in light green. A). Apa-Apa forest and B) Cala-Cala forest. Yellow points indicate the study sites.

During the last decades, montane forests in the study area have been deforested and fragmented due to high levels of selective logging and deliberate fires for the expansion of coca (*Erythroxylum coca*) fields. Nowadays, continuous forest areas are only found on mountain tops surrounded by huge burned areas dominated by bracken (i.e., *Pteridium arachnoideum*) and secondary woody species (i.e., *Miconia, Rubus, Mirsine*) (**Figure 2**). Currently, two large forest remnants remain in the vicinity of Chulumani: one is a private ecological reserve under the administration of a local community (Apa-apa forest 10° 20’ 50.60’’ S 67° 30’ 48.46’’ W) and the other is an unprotected forest remnant (Cala-cala forest 16° 24’ 39.12’’ S 76° 34’ 00.91’’ W) (**Figure 1**). Both forest remnants have an extension of approximately 3000 ha

(Gallegos et al. 2014). Except for these remaining forests, the zonal vegetation has disappeared at this altitudinal belt.

Figure 2. Tropical montane forest in northern Bolivia disturbed by deforestation. a) Fragmented landscape, b) Continuous forest and deforested habitats dominated by bracken (*Pteridium arachnoideum*), c) Human-induced forest edge at the forest-bracken transition zone.

A species inventory carried out by S.G. Beck (Unpublished data) revealed that these forests could host thousands of species. Thus far, 259 woody plant species belonging to 58 families have been recorded in the area (Lippok et al. 2013a). The most common species in the forest are *Clusia lechleri, Clusia sphaerocarpa, Clusia trochiformis* (Clusiaceae Lindley), *Myrsine coriacea* (Primulaceae R. Brown), *Clethra scabra* (Clethraceae Klotzsch), *Weinmannia pinnata* (Cunoniaceae R. Brown) and *Hyeronima cf. laxiflora* (Euphorbiaceae A.L. de Jussieu) (**Figure 3**). The forest has a mean canopy height of 15-20 m divided into three vertical strata (Navarro & Maldonado 2002).

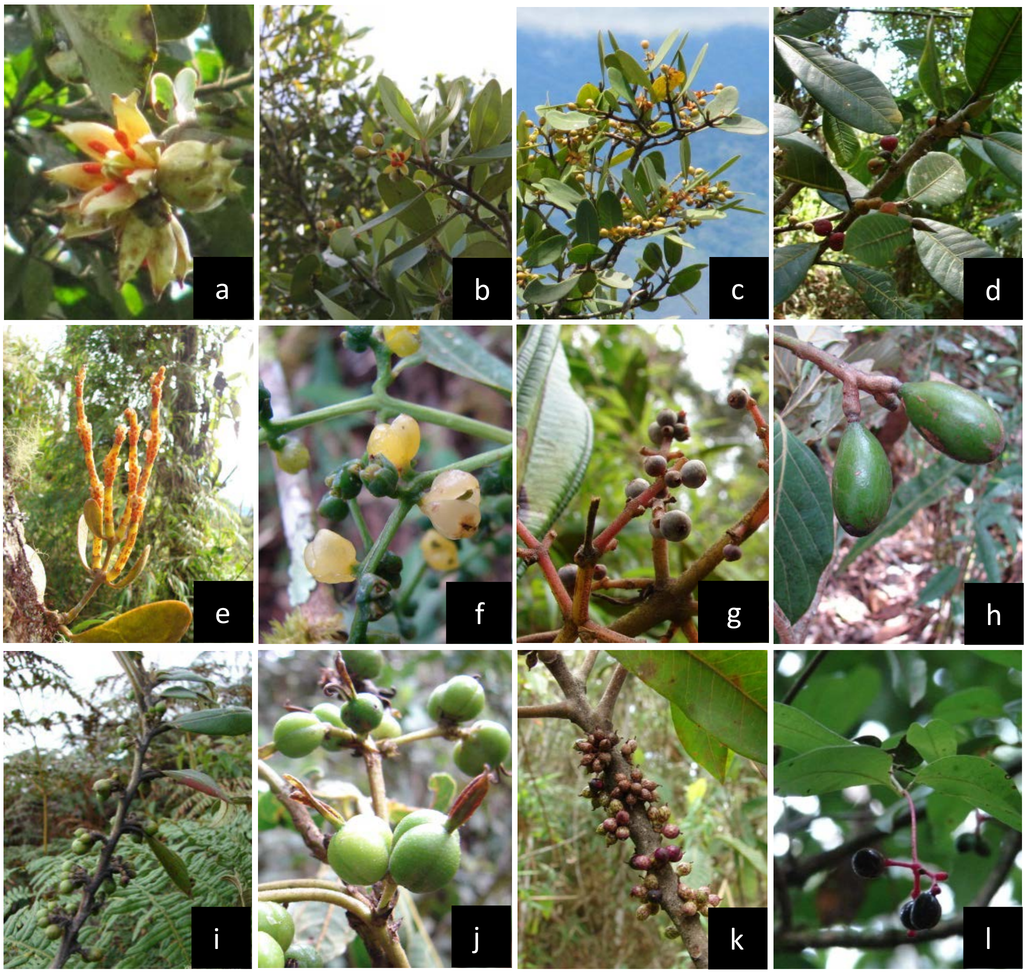

Figure 3. Fleshy-fruited plant species consumed by frugivorous birds. a) *Clusia sphaerocarpa*, b) *Clusia trochiformis*, c) *Clusia lechleri* (all Clusiaceae), d) *Ficus america* (Moraceae), e) *Dendrophthora macbridei* (Viscaceae), f) *Hedyosmun racemosum* (Chloranthaceae), g) *Miconia* cf. *brittoni* (Melastomataceae), h) *Beilschmiedia tovarensis* (Lauraceae), i) *Freziera lanata* (Theaceae), j) *Alchornea triplinervia* (Euphorbiaceae), k) *Myrsine coriaceae* (Primulaceae) and l) *Faramea candelabrum* (Rubiaceae). Foto credits: Avalos V. and Gallegos S.

Frugivorous birds are the most important animal seed dispersers in the study area, as it is typically found in neotropical mountain systems (Herzog et al. 2005b). For the specific altitudinal gradient in the "Yungas" area, I recorded 120 bird species of which 47 species (39 %) were observed feeding on fruits. Among the most important families of frugivorus birds are Thaupidae, Parulidae, Cotingidae and Tyranidae. The most abundant frugivorous bird species are *Tangara vassorii, Tangara xanthocephala, Thraupis cyanocephala, Anisognathus somptuosus* (all

Thraupidae), *Mionectes striaticollis* (Tyranidae), *Pyrrura molinae* (Psittacidae) and *Chiroxiphia boliviana* (Pipridae) (Saavedra et al. 2014, additionally see Remsen 1985 for a gradient between 3050-3300 m for a similar montane forest) (**Figure 4**). A large majority of individual birds seen foraging in fruiting trees were part of mixed- or single-species flocks.

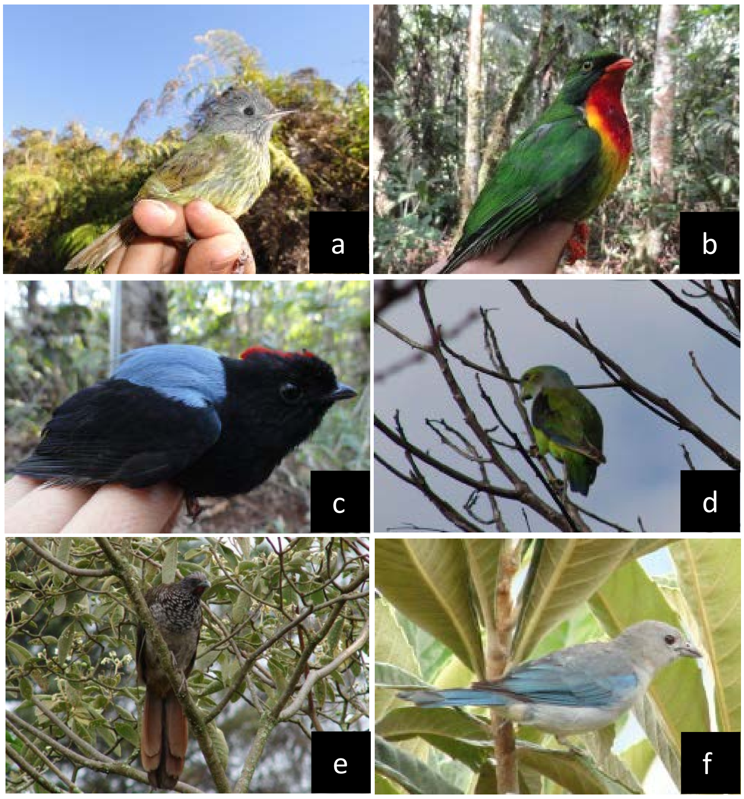

Figure 4. Frugivorous bird species observed feeding on fruits in the study area in Bolivia: a) *Mionectes striaticollis* (Tyranidae), b) *Pipreola frontalis* (Cotingidae), c) *Thraupis sayaca* (Thraupidae), d) *Chiroxiphia boliviana* (Pipridae), e) *Hapalopsittaca melanotis* (Psittacidae), f) Penelope montagnii (Cracidae). Foto credits: Avalos V. and Villegas M.

Chapter 2 – Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed dispersal networks

Francisco Saavedra, Isabell Hensen, Stephan Beck, Katrin Böhning-Gaese, Denis Lippok, Till Töpfer & Matthias Schleuning

Oecologia (2014) 176: 837-848

Abstract

Although seed dispersal networks are increasingly used to infer the functioning of ecosystems, few studies have investigated the link between the properties of these networks and the ecosystem function of seed dispersal by animals. We investigate how frugivore communities and seed dispersal change with habitat disturbance and test whether relationships between morphological traits and functional roles of seed dispersers change in response to human-induced forest edges. We recorded interaction frequencies between fleshy-fruited plants and frugivorous bird species in tropical montane forests in the Bolivian Andes and recorded functional bird traits (body mass, gape width and wing tip length) associated with quantitative (seed removal rate) and qualitative (seed deposition pattern) components of seed dispersal effectiveness. We found that the abundance and richness of frugivorous birds were higher at forest edges. More fruits were removed and dispersed seeds were less clustered at edges than in the interior. Additionally, functional and interaction diversity were higher at edges than in the interior, but functional and interaction evenness did not differ. Interaction strength of bird species increased with body mass, gape width and wing tip length in the forest interior, but was not related to bird morphologies at forest edges. Our study suggests that increases in functional and interaction diversity and an even distribution of interaction strength across bird morphologies lead to enhanced quantity and tentatively enhanced quality of seed dispersal. It also suggests that the effects of species traits on ecosystem functions can vary along small-scale gradients of human disturbance.

Keywords: Ecosystem functioning, functional diversity, morphological traits, montane forest, plant-frugivore interactions.

Chapter 3 – Seed-deposition patterns are unrelated to plant recruitment in a disturbed tropical montane forest in Bolivia

Francisco Saavedra, Isabell Hensen, Amira Apaza, Eike Lena Neuschulz & Matthias Schleuning

Submitted to Biotropica on 27/03/2014 and invited for resubmission on 16/07/2014

Abstract

Spatial patterns of seed dispersal and recruitment of fleshy-fruited plant species in tropical ecosystems are thought to be mainly driven by seed deposition by animal seed dispersers. To test this notion, we studied the relationship between seed deposition and seedling recruitment patterns of three sympatric species of *Clusia* in a tropical montane forest of the Bolivian Andes and tested whether this relationship changes between habitat types and different recruitment stages. We recorded (1) the number of seeds deposited in seed traps to assess the seed-deposition pattern and (2) the abundance of recruits to evaluate the spatial pattern of recruitment stages in 14 plots at seven sites. We found that more fruits were removed and deposited by frugivorous birds at the forest edge than in the interior. The number of deposited seeds decreased with increasing distance from the focal fruiting tree in both habitat types. The density of 1-yr-old seedlings, saplings and adult trees were higher at forest edges, whereas densities of 2-yr-old seedlings were similar in both habitat types. While seedlings were randomly distributed, saplings and adult trees were more clustered than expected from a random distribution. Differences in the spatial recruitment patterns between recruitment stages suggest impacts of environmental filters, such as water and light availability, which are unrelated to the initial seed-deposition pattern. We conclude that in human-disturbed forests the initial seed-deposition pattern generated by frugivorous animals can be disconnected from plant recruitment patterns, which has important implications for plant community dynamics and species coexistence in these forests.

Keywords: *Clusia*; forest edge; frugivorous birds; recruitment stages; seed dispersal; seedling establishment.

Chapter 4 – Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forest

Francisco Saavedra, Isabell Hensen & Matthias Schleuning

Submitted to Applied Vegetation Science on 14/10/2014, currently under *review*

Abstract

Questions: (1) How do seed abundance and species richness change from forest interior to deforested habitats? (2) Are seed abundance and species richness of seed species dispersed into deforested areas enhanced by the presence of perch structures? (3) Do morphological seed traits of forest and non-forest plant species change from the forest interior to deforested areas?

Location: Deforested tropical mountains of Chulumani, La Paz, Bolivia.

Methods: At eight study sites, we installed a system of 38 seed traps along a transect of 250 m from the forest interior (160 m distance from the forest margin) toward deforested areas (80 m distance from the forest margin). Half of the seed traps installed in the deforested areas were positioned under perch structures. We identified captured seeds to morpho-species or species level and recorded morphological seed traits (i.e., seed mass, seed length, seed width) and species origin (i.e., late-successional, pioneer, non-forest species) for all seed species.

Results: Seed abundance and species richness decreased strongly from the forest interior toward deforested areas. Seed limitation was particularly strong for large-seeded and late-successional species. Perches in deforested areas strongly increased the abundance and to some extent also the species richness of seeds dispersed into these areas, but did not alter the composition of seed traits and species origin in comparison to seed traps without perches.

Conclusions: We found a strong seed dispersal limitation toward deforested areas, which was mitigated by the presence of perch structures, at least in terms of seed abundance and species richness. However, the dispersal limitation of late-successional plant species with large seeds was not compensated by the presence of perching structures. The establishment of artificial perching structures could be a promising strategy for enhancing seed dispersal into deforested areas and for establishing foci of regeneration in the long term.

Keywords: Bolivia; distance to source habitat; forest recovery; frugivorous birds; montane forest; perch structures; seed dispersal limitation; seed traits

Chapter 5 – Synthesis

General discussion

The aim of the thesis is to investigate the association between functional diversity (FD) of frugivorous bird species in seed dispersal networks with quantitative and qualitative components of SDE in human-disturbed forest. I tested whether functional traits determine quantity and quality of SDE and whether this relationship changes with the influence of human disturbance. My results reveal that components of SDE are determined by the functional diversity of avian-seed dispersers and that human disturbance modifies the functional role of avian-seed dispersers and the spatial distribution of functional seed traits in deforested habitats. With this study, I suggest that an increased functional diversity of avian seed dispersers and an increased diversity of species interactions at forest edges play a central role in determining the quantitative component of seed dispersal at forest edges. However, the effects of deforestation also affected the qualitative component of SDE by modifying the spatial pattern of dispersed seeds, recruits and the composition of seed traits. In this sense, our understanding on how SDE is related to the functional diversity of seed dispersers in seed dispersal networks is critical to expand our comprehension of the ecosystem function of seed dispersal by frugivorous birds. Tentatively, my findings suggest that the quantitative components of seed dispersal may be more easily to restore in deforested habitats than the qualitative components related to seed-deposition patterns. Thus, the application of my results may also be helpful to develop active forest restoration techniques that take into account the contribution of the remaining assemblages of plant and bird species to restore the functionality of disturbed habitats.

Functional diversity in seed dispersal networks

This thesis reported for the first time a positive relationship between the diversity of species interactions and the functional diversity of frugivorous bird species in seed dispersal networks (**Chapter 2**). This suggests that a functional diverse assemblage of bird species will generate a more diverse and complex seed dispersal network. Several studies on seed dispersal networks in temperate (Perea et al. 2012, García et al. 2013) and tropical (Schleuning et al. 2011, Menke et al. 2012) ecosystems documented the pivotal role of seed dispersal interactions for community dynamics.

Moreover, studies about the differential response of frugivorous species to human disturbance found that interaction frequencies between frugivorous bird and fleshy-fruited plant species may change at forest edges (Restrepo et al. 1999, Galetti et al. 2003). Effects of human disturbance may alter the structure of seed dispersal networks (Menke et al. 2012) by changing the relationship between functional traits and species interaction strength (Perea et al. 2012). Here, I found a positive relationship between morphological traits and interaction strength of bird species, but only in the forest interior. By contrast, at the forest edge there were no significant relationships between bird traits and interaction strength (**Chapter 2**). Effects of morphological traits on the strength of species interactions have previously been found in pollination networks (Junker et al. 2013), but are less studied for seed dispersal networks (Schleuning et al. 2011, Perea et al. 2012, Dehling et al. 2014). My results suggest that morphological bird traits may influence seed dispersal effectiveness. For instance, (1) body mass may determine the dispersal distance and the number of fruits consumed per seed disperser (Wotton & Kelly 2012), (2) the wing tip length will determine the mobility of seed dispersers and thus seed dispersal patterns (Böhning-Gaese et al. 2006) and (3) the gape width will determine morphological limitations to swallow and disperse fruits (Wheelwright 1993). The even contribution of bird species with different morphologies to seed dispersal may contribute to enhance quantity and, to some extent, quality of seed dispersal at forest edges. Because morphologically distinct bird species are characterized by differences in movement behaviour (Sun et al. 1997, Westcott & Graham 2000), home ranges (Haskell et al. 2002) and habitat preferences (Fonderflick et al. 2013), we can expect that this variability in functional roles might increase the functional complementarity among seed disperser species (Jordano et al. 2007, Lehouck et al. 2009, Morales et al. 2013), generating a less clustered seed deposition pattern. By contrast, the large contribution of morphologically similar bird species in the forest interior may increase the functional redundancy and may lead to a more clustered seed dispersal pattern. However, the importance of large-bodied species in the forest interior also reflects the unique role of these species for both quantitative and qualitative seed-dispersal components in tropical forests (Wotton & Kelly 2012, Galetti et al. 2013).

SDE after deforestation

I revealed the role of deforestation as a main driver for quantitative and qualitative SDE components in human-disturbed forest. Most studies in tropical forests found negative effects of human-disturbance on quantitative and qualitative components of SDE (de Melo et al. 2006, Sodhi et al. 2004) and seed dispersal vectors (Jacomasa & Pizo 2010, Loayza & Knight 2013). However, recent studies in disturbed tropical montane forest found evidence that human-induced forest edges may have positive effects on quantitative and qualitative components of SDE by increasing the abundance and diversity of frugivorous birds (Babweteera & Brown 2009, Menke et al. 2012) and the diversity of fleshy-fruited plant species (Fontoura et al. 2006). Species richness will increase the quantity of visits to fleshy-fruited plant species by frugivorous birds (i.e., frequency of interaction events between pairs of species) (Bascopte & Jordano 2007, Vázquez et al. 2009). Similar trends were found at forest edges in Kenyan rain forests disturbed by selective logging (Menke et al. 2012). Also, secondary effects of increased diversity of fleshy-fruited plant species contribute to increase the number of visits, due to higher diversity and availability of food resources (Vázquez et al. 2007, Alberti & Morellato 2010, Carlo & Yang 2011). Accordingly, in my study, more fruits were consumed at forest edges and this effect was positively associated with the production of food resources (**Chapter 2**). Similarly Herrera et al. (1994) found that fruit production increased fruit removal in a temperate forest. The number of seeds consumed per visit is related to the complementarity of functional traits of interacting bird (*i.e.,* body mass, gape with) and plant (*i.e,.* fruit size, seed size) species (Jordano 2000, Santamaría & Rodriguez-Gironés 2007). Fruit removal from parental trees is a crucial factor for the quantitative component of SDE of avian-dispersed plant species, since seed mortality is often high under and beneath parent trees (e.g., distance- and density-dependent mortality) (Janzen 1970, Janzen 1971, Böhning-Gaese et al. 1999). A high number of fruits consumed by frugivorous seed dispersers may thus be reflected by an increased number of seeds dispersed in the landscape. The quality of the spatial distribution of dispersed seeds generated by frugivorous birds is further influenced by additional factors, such as the diversity of the local bird assemblage (Jordano et al. 2007), feeding behaviour (Moermond & Denslow 1985, Foster 1987) and movement patterns (Lenz et al. 2010) which, in turn, may depend on habitat conditions (Breitbach et al. 2012a). Consequently, the more widely the seeds are dispersed in space, the greater are the chances that seeds reach suitable sites for establishment (Babweteera & Brown 2009).

At population level, the quality of the seed deposition pattern (*i.e.,* seed shadows) was similar between habitat types, but differed significantly at mid-distances close to the margin of the tree crown (*i.e.,* at 8 m from the tree crown) (**Chapter 3**). I found that the abundance of seeds concentrates under fruiting trees and declines rapidly with the distance to the tree crown. Similarly, numerous studies in the tropics reported that animal-dispersed seeds decline in abundance with increasing distance to the parental trees (Izhaki et al. 1991, Koike et al. 2010). In general, animal dispersed plant species tend to have more clustered seed deposition patterns than abiotically dispersed plant species (Muller-Landau et al. 2008). Although a diverse assemblage of bird species with different morphologies may contribute to increase the quantity of seed dispersal and generate a less clustered seed deposition pattern (Jordano et al. 2007, Calviño-Cancela & Martin-Herrero 2009, Morales et al. 2013), animal-mediated seed dispersal in *Clusia* resulted in a clustered seed deposition pattern (**Chapter 3**). My results suggest that the local seed-deposition pattern of *Clusia* was mostly shaped by post-foraging behaviour of their main seed dispersers, as was found in previous studies (Carlo et al. 2003, Carlo & Tewksbury 2014). The highly clustered seed deposition pattern under *Clusia* trees could be associated with the high number of seeds captured under tree crowns as a result of several null-dispersal events (Breitbach et al. 2012b), whereas seeds dispersed outside the tree crown were the consequence of delimited seed dispersal movements, probably mostly conducted by their main seed dispersers (*i.e., Mionectes striaticollis* and *Chiroxiphia boliviana*). Similar movement patterns were recorded by Sun et al. (1997) in tropical montane forest of Rwanda for three species of turacos (*Corythaeola cristata*, *Musophaga johnstoni* and *Tauraco schuettii*, Musophagidae) and by Westcott and Graham (2000) for *Mionectes oleagineous* in Costa Rica. The high contribution of small-bodied bird species implies that the generated seed deposition pattern was highly clustered close to fruiting trees (Babweteera & Brown 2009). Although I did not register the flight distance of seed dispersers after fruit consumption, I observed that about 80% of bird destinations after foraging were close to the fruiting trees where frugivorous birds perched and defecated seeds. Flight destinations were mostly directed to neighboring trees and this movement behavior may explain the high number of seeds dispersed just outside the crown of fruiting trees. This is consistent with previous studies that reported that post-foraging movements of seed dispersers affect the distance that seeds are dispersed (Moermond & Denslow 1985, Foster 1987) and that these movements may be associated with functional bird traits, such as wing tip length, and the configuration of disturbed habitats (Breitbach et al. 2010a).

The high number of seedlings established at the forest edge was consistent with the high number of seeds deposited in the same habitat type (**Chapter 3**). However, the seed deposition pattern generated by their main seed dispersers was disconnected with the recruitment pattern of newly germinated seedling as found in previous studies (Calviño-Cancela & Martin-Herrero 2009, Spiegel & Nathan 2012). The spatial pattern of seedlings followed an almost random distribution, probably due to the seed dispersal pattern generated by the avian frugivores around fruiting trees of *Clusia*, whereas the spatial structure of juveniles and adult trees followed a clustered distribution, possibly due to differential effects of environmental conditions on recruitment stages (**Chapter 3**). Some studies suggest that the decrease in the abundance of individuals with age mostly results from density-dependent mortality due to intraspecific competition (Harms et al. 2000, Metz et al. 2010) or detrimental environmental conditions (Fenner & Thompson 2005). By contrast, survival rates may increase with plant age and size (de Steven 1994). In consequence, early recruitment stages such as newly germinated seedlings are more prone to die during the first year of life. In our system, differences in the abundance of individuals between the two seedling stages (newly germinated and 2-yr-old seedlings) may be mostly due to abiotic conditions at sites where seeds arrive and germinate (Cavallero et al. 2012), rather than to post-dispersal processes, such as seed predation or herbivory. A study conducted in the same study area found low rates of seed predation at forest edges for *Clusia* seeds (Gallegos et al. 2014). However, fluctuations in local environmental conditions (i.e. less humidity and high temperatures) between habitat types could cause a massive mortality of seedlings, due to desiccation (Comita & Engelbrecht 2009), and are likely to modify the initial seed dispersal pattern. Abiotic filters such as an open canopy and stressful environmental conditions at locally disturbed sites could have limited the transition of individuals from the first (newly germinated) to the second seedling stage (2-yr-old seedlings). Similarly, seedling establishment limitation was found by Valdes & García (2013). By contrast, increased light availability in disturbed habitats may have positive effects on later recruitment stages. For instance, the number of saplings recorded in plots of 2 x 20 m growing larger than 2 m tall was much greater at the forest edges than in the forest interior (47 % vs. 17 % of saplings >2 m, respectively). This suggests that saplings in disturbed habitats grew faster than individuals in the forest interior, probably due to the higher light availability at the forest edge (Lippok et al*.* 2013c). High light availability could also increase the abundance of individuals recruited to the sapling stage at forest edges (**Chapter 3**). These examples suggest that abiotic rather than biotic environmental conditions may act as filters on the recruitment of plants and generate differences in the recruitment pattern between habitats and recruitment stages, at least in my study system. Furthermore, it suggests that habitat conditions may cause recruitment conflicts between stages (Schupp 2007) and may be a limiting factor for population growth.

At community level, the seed deposition pattern (*i.e.,* seed rain) changed between habitat types (**Chapter 4**) and was shaped by the limited number of mid- and long-distance seed dispersal events from forested to deforested habitats (Holl 1999, Holl et al. 2000). As a consequence the seed rain pattern was functionally depauperate in deforested habitats, probably due to the limited use of these areas by large-bodied seed dispersers (*i.e.,* limited number of seed dispersal events). I found that seeds where mostly dispersed until 10 m outside the seed source habitat (*i.e.,* forest edge), whereas seed species richness declined continuously from the forest interior toward deforested areas, indicating that avian frugivores failed to disperse seeds far away from the seed source habitat (**Chapter 4**). The reduced number of seeds and species of late-successional forest species in deforested areas (only comprising 9 % of the species of all dispersed seeds) highlights the negative effect of deforestation on seed dispersal, confirming previous studies in other tropical deforested areas (Costa et al.

2012). This may lead to a strong seed dispersal and establishment limitation of forest regeneration (Günter et al. 2007, Dosch et al. 2007). Seed dispersal limitation may also be related to the absence of perching structures in deforested areas. Effects of seed dispersal failure toward deforested habitats changed the composition of morphological seed traits, such as seed mass, seed width and seed length, from the forest interior to deforested areas (**Chapter 4**). A similar pattern was also reported by de Melo et al. (2006) in the Brazilian Atlantic forest. This suggests that deforestation could have strong negative effects on the structure and composition of seed traits at small scales (*i.e.,* distances) and between forested and deforested habitats (Lopes et al. 2009). In **Chapter 2**, I demonstrated that an even distribution of interaction strength across bird morphologies enhanced quantity and tentatively also the quality of seed dispersal at forest edges. Thus, at the edges, small frugivores are relatively more important than in the forest interior. Accordingly, I found more small than large seeds outside the forest (**Chapter 4**), indicating that specific seed traits were lost at forest edges and toward deforested areas (Girao et al. 2007, Lopes et al. 2009). Because morphological bird and seed traits in the respective assemblages changed in response to human disturbance, small seeds were mostly dispersed close to the forest margin and under perching structures in deforested areas, mostly by small frugivorous birds. Supporting this idea, Ingle (2003) and Menke et al. (2012) also found that smaller seeds were more likely to be dispersed to successional areas by small frugivorous birds in montane rainforest.

Incentives for forest restoration

Perching structures have a positive effect on seed dispersal into deforested habitats. Because regeneration processes in deforested habitats are hampered by seed dispersal limitation (Hooper et al. 2005, Pejchar et al. 2008), the presence of remnant trees or perching structures is important for starting forest regeneration. Seed dispersal limitation is due to few seed dispersal events of fleshy-fruited plant species into disturbed areas (Wotton & Kelly 2011). For instance, Silva et al. (1996) reported that few seeds were dispersed far from the forest edge because few frugivorous bird species were able to spent long time in abandoned pastures, due to the absence of perching structures. The distance that seeds can be dispersed toward disturbed habitats is associated to the availability of perching structures that facilitated the movement of avian seed dispersers into these habitats (Holl 1998, Galingo-González et al. 2000, Herrera & García 2009, Heelemann et al. 2012, Graham & Page 2012). Although I did not routinely follow the movements of seed dispersers after fruit consumption, several small frugivorous bird species with high numbers of visits and dispersed seeds per visit (**Chapter 2**), such as *Mionectes striaticollis*, *Tangara vassorii, Tangara xanthocephala*, *Thraupis cyanocephala,* and *Thraupis sayaca,* were observed flying toward perching structure in deforested areas, but they hardly stopped there for long time. Thus, seed dispersal toward perching structures in deforested habitats is crucial for seed dispersal because other sources of regeneration such as the seed bank usually decline with increasing distance from the forest edge and are therefore a poor source for forest regeneration (Zimmerman et al. 2000, Lippok et al. 2013b). In our study system, seed abundance increased strongly, whereas seed species richness of animal-dispersed forest species slightly increased under perching structures in comparison to deforested areas without perches (**Chapter 4**). Similar patterns were found in tropical disturbed habitats in Indonesia (Blackham et al. 2013) and South Africa (Heelemann et al. 2012). Thus, the role of perching structures will reduce seed dispersal limitation and potentially increase establishment of dispersed seeds. Since many studies highlighted the importance of perch structures and pioneer species as drivers of forest restoration (Galindo-González et al. 2000, Heelemann et al. 2012), the establishment of local pioneer species that produce large amounts of fleshy fruits may attract animal seed dispersers to deforested areas (Wunderle 1997). In the short term, this could increase the visitation rates of frugivorous bird species to the deforested area. In the long term, the presence of perches may increase the probabilities of forest regeneration by increasing seed deposition, also of late-successional tree species. Nevertheless, seed addition of large-seeded late-successional species may additionally be needed, due to the lack of large seeds dispersed by frugivorous birds into the deforested areas.

Outlook

This study is among the first attempts to analyze the SDE framework from a functional perspective. It is also one of the first studies linking functional diversity of seed dispersers and avian-seed dispersal networks. I demonstrate that quantitative and qualitative components of SDE are influenced by the functional diversity of seed dispersers and the structure of seed dispersal networks. The quantitative component of SDE is highly dependent on the redundancy and complementarity (Bueno et al. 2013) of species traits and the abundance of individuals in the assemblage of interacting species (Díaz & Cabido 2001). The qualitative component of seed dispersal is also related to the functional diversity of the assemblage of seed dispersers (Westcott & Graham 2000, Russo et al. 2006). Although the SDE framework was frequently studied during the last two decades, our comprehension of the qualitative components of the ecosystem function of seed dispersal is still limited (but see García et al. 2012). Thus, it is important to conduct more spatially explicit analyses of seed dispersal that improve our understanding of the effects of seed deposition patterns on plant demography (see also García et al. 2013). I suggest that assessing the functional diversity of the entire assemblage of seed dispersers within the SDE framework can provide a more comprehensive and realistic evaluation of the ecosystem function of seed dispersal. This approach may expand our understanding of the functional role of seed dispersers in plant-frugivore networks and their ultimate effects on SDE. To this end, more work is needed about the functional role of seed dispersal and its significance for ecosystem functioning (Wenny et al. 2011). Approaches such as those linking biodiversity and ecosystem functioning (BEF) (Loreau et al. 2001) with plant-animal mutualistic networks (Schleuning et al. 2014b), including the link to forest restoration (Aerts & Honnay 2011), are fundamental to understand how ecological processes contribute to forest restoration in the tropics and elsewhere. A major future line of study should, therefore, be to integrate mutualistic interaction networks (*e.g.,* seed dispersal, pollination), functional diversity (*i.e.,* trait-based approaches) and plant recruitment dynamics (*i.e.,* seed dispersal loop, plant demography).

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Appendix A

Curriculum vitae

Personal information

Name: Francisco Vicente Saavedra Agramont
Date of birth: 20.02.1982
Place of birth: Sorata, Bolivia
e-mail: saavedragramont.francisco@gmail.com

Education

2010 - actual	Ph.D. student at Martin_Luther Halle-Wittenberg University (MLU), Institute of Biology, Halle, Germany and Biodiversity and Climate Research Center (BiK- F), Frankfurt am Main, Germany. Topic "*Seed dispersal by birds in tropical montane forests: towards a functional understanding of seed dispersal effectiveness after deforestation*". Supervisors: Isabell Hensen (MLU) and Matthias Schleuning (BiK-F).
2009	Diploma in Organic Agriculture. Escuela de Medio Ambiente y Energía del Instituto Latinoamericano de Ciencias, Perú. Topic: "*The forest as a source of polinators in the production of fruits of Theobroma cacao in Alto Beni, Bolivia*". Supervisor: Dr. Renate Seidel.
2008	Licentiate in Biology*. Universidad Mayor de San Andrés (UMSA), La Paz, Bolivia. Topic "*Recruitment patterns – dispersal, survival and establishment– of Guettarda viburnoides in savannas of the Biosphere Reserve Station Biologica del Beni (RB-EBB)*". Supervisors: Dr. Mónica Moraes (UMSA) and Dr. Andrea Loayza.

* Licenciatura: equivalent to a Master degree.

Work experience

2008 – 2009	Consultant in environmental passives. General department of environment. Vice ministry of Biodiversity, Forestal Resources and Environment. Ministry of Rural Development, Agriculture and Environment.

2008	Research assistant of the project “Pollination biology of two long-lived columnar cactus in the prepuna biogeographical region”.
2007	Research assistant in the Herbario Nacional de Bolivia. Jardín Botánico.
2007	Teaching assistant of General Biology (BIO-101). Biology career, Faculty of Natural Science, Universidad Mayor de San Andrés (UMSA).
2007	Teaching assistant of Vegetal Physiology and Ecophysiology (BOT-302) Biology career, Faculty of Natural Science, Universidad Mayor de San Andrés (UMSA).
2005-2006	Field assistant in the Project “Biodiversity in the Bermejo River basin”.
2005	Research assistant in the Herbario Nacional de Bolivia. Jardín Botánico.

Publications of the dissertation

Saavedra, F., Hensen I., Beck S., Böhning-Gaese K., Lippok D., Töpfer, T & M. Schleuning (2014) Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed dispersal networks. *Oecologia* **176**: 837-848

Saavedra, F., Hensen I., Apaza A., Neuschulz E. & M. Schleuning (Manuscript). Seed-deposition patterns are unrelated to plant recruitment in a disturbed tropical montane forest in Bolivia. Submitted to Biotropica on 27/03/2014 and invited for resubmission on 16/07/2014.

Saavedra, F., Hensen, I. & M. Schleuning (Manuscript) Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forests. Submitted to Applied Vegetation Science on 14/10/2014, currently under *review*.

Additional publications

Gallegos, S.C., Hensen, I., **Saavedra, F.** & 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

Schleuning, M., Ingmann, L., Strauβ, R., Fritz, S.A., Dalsgaard, B., Dehling, M.D., Plein, M., **Saavedra, F**., Sandel, B., Svenning, J.C., Bohning-Gaese, K., C. Dormann (2014) Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters* **17**: 454-463.

Apaza Quevedo A., Schleunig, M., Hensen, I., **Saavedra, F**. & Durka,. W. (2013) Forest fragmentation and edge effects on the genetic structure of Clusia sphaerocarpa and C. lechleri (Clusiaceae) in tropical montane forests. *Journal of Tropical Ecology* **29**: 321-329.

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

Contribution to conferences

Saavedra F., Hensen I., Beck S., Böhning-Gaese K., Lippok D., Töpfer T & M. Schleuning (2014) “The fuctional importance of seed dispersers changes at forest edges”. IV Congreso Boliviano de Ecología, Santa Cruz, Bolivia. Oral presentation.

Saavedra F., Hensen I., & M. Schleuning. “Plant-frugivore interaction networks in tropical montane forest”. III Congreso Boliviano de Ecología. Sucre, Bolivia. Poster presentation.

Appendix B

Erklärung über den persönlichen Anteil an den Publikationen

Study 1 (Chapter 2):

Francisco Saavedra, Isabell Hensen, Stephan G. Beck, Katrin Böhning-Gaese, Denis Lippok, Till Töpfer & Matthias Schleuning (2014): Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed dispersal netwoks. *Oecologia,* 176: *837-848.*

Data collection: **Francisco Saavedra** (80%), Stephan G. Beck (10%), Till Töpfer (10%)
Analysis: **Francisco Saavedra** (60%), Matthias Schleuning (40%)
Writing: **Francisco Saavedra** (70%), Matthias Schleuning (30%),
comments and edits on the first manuscript draft by Stephan G. Beck, Isabell Hensen, Katrin Böhning-Gaese, Denis Lippok

Study 2 (Chapter 3):

Francisco Saavedra, Isabell Hensen, Amira Apaza, Eike Lena Neuschulz & Matthias Schleuning: Seed-deposition patterns are unrelated to plant recruitment in a disturbed tropical montane forest in Bolivia. Submitted to Biotropica on 27/03/2014 and invited for resubmission on 16/07/2014.

Data collection: **Francisco Saavedra** (80%), Amira Apaza (20%)
Analysis: **Francisco Saavedra** (70%), Matthias Schleuning 30%)
Writing: **Francisco Saavedra** (70%), Matthias Schleuning (30%),
comments and edits on the first manuscript draft by Stephan G. Beck, Isabell Hensen and Eike Lena Neuschulz

Study 3 (Chapter 4):

Francisco Saavedra, Isabell Hensen & Matthias Schleuning: Deforested habitat lack seeds of late-successional and large-seeded plant species in tropical montane forest. Submitted to Applied Vegetation Science on 14/10/2014, currently under *review.*

Data collection and laboratory work: **Francisco Saavedra** (100%)
Analysis: **Francisco Saavedra** (70%), Matthias Schleuning (30%)
Writing: **Francisco Saavedra** (70%), Matthias Schleuning (30%),
comments and edits on the first manuscript draft by Isabell Hensen

Applicant and corresponding author: Halle, 02.12.2014

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "**Seed dispersal by animals in tropical montane forests: towards a functional understanding of seed-dispersal effectiveness after deforestation**" 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.

Unterschrift: ____ (Francisco V. Saavedra)

Halle (Saale), den 2.12.2014