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STRESS GRADIENTS - DRIVERS OF FUNCTIONAL DIVERSITY AND GENETIC PATTERNS OF WOODY SPECIES IN TROPICAL MONTANE FOREST (BOLIVIA)

A LINK TO EDGE EFFECTS

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Cover photo

View of a fragmented landscape in the province of Sud Yungas, Bolivia (photo by A. Apaza)

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CONTENTS

SUMMARY

Forest fragmentation as a result of changes in land use constitutes an important driver for global change. In tropical montane forests, it is common to use fire for agricultural practices in order to clear land and to grow crops. Often these fires get out of control and extend to the forest, thus contributing to a permanently fragmented forest configuration with huge forest edges. Although tropical montane forests already exhibit a high environmental heterogeneity, mainly attributed to elevation and topography, human induced edge effects create an additional environmental gradient. Former studies have shown how elevation and topography affect composition and structure of plant communities but rarely do they consider different components of functional diversity. Leaf traits associated to resource use strongly determine plant success along environmental gradients and can be important indicators of species distributions and assemblages. Thus, connecting functional diversity information to responses of plant communities to natural and induced gradients of stress may help to understand mechanisms that shape species distributions and warn about potential consequences of changes in the environment. Furthermore, other studies have also shown that edge effects extend to species interactions as pollination and seed dispersal. Considering the high influence of these interactions on the gene flow of tropical plant species, it would be expected that impacts of edge effects could even extend to the genetic structure of plant species.

Using montane forests of the Bolivian Andes as a model system, this thesis study aims at contributing to our understanding how natural and human induced gradients of stress drive both functional traits and genetic structure of woody species. The first study evaluates relationships between environmental variables and leaf traits associated with resource use strategies as well as variations of functional composition and structure with regard to elevation, topography and edge effects. I found that leaf traits associated with resource use are responsive to soil properties rather than to microclimate variables, which supports the importance of soil as a driver of changes in functional composition in these forests. The dominance of species with a conservative resource use strategy in more stressed habitats such as those at high elevation, ridges and forest edges showed the importance of stress as a driver of functional traits and species distribution. Since decomposition and productivity have shown to respond to changes in leaf traits associated with resource use, these results also warn about effects of induced environmental changes resulting from fragmentation on the ecosystem functioning. The maintenance of functional structure across the different stress gradients suggest a role of less abundant species as buffer of stress effects and this highlights the significance of functional redundancy in species-rich communities.

The second study evaluates edge effects on the genetic structure and fine-scale spatial genetic structure (SGS) of two animal dispersed species. Genetic differentiation between populations of *Clusia sphaerocarpa* and *Clusia lechleri* at edges and forest interior indicate that induced environmental changes such as edge effects can drive genetic divergence even at small geographical scale. This highlights the importance of habitat dissimilarity as a driver of genetic differentiation. Higher SGS in forest interior as compared to forest edges most probably results from an increase in seed dispersal and population sizes of *Clusia* species, which is favored at forest edges and indicate a break-up of local genetic structures.

This thesis contributes novel information about the role of fragmentation inducing gradients of stress in tropical montane forests and its impact on functional diversity and genetic structure of plant woody species. Thus, edge effects showed to affect on multiple levels of species organization, up from species distributions down to their fine scale spatial genetic structure. These extensive consequences should be included when assessing the impact of further land-use decisions and conservation programs.

ZUSAMMENFASSUNG

Im Zuge der Intensivierung verschiedener Landnutzungsformen werden bestehende Wälder häufig gerodet und an den entstandenen Waldfragmente bilden sich oft starke Umweltgradienten heraus. In tropischen Bergwäldern ist die Brandrodung eine übliche Praxis zur Urbarmachung des Bodens für landwirtschaftliche Nutzung. Die Feuer geraten häufig außer Kontrolle und erfassen dann auch Wälder die nicht für die Rodung bestimmt waren. Somit tragen diese Feuer zur dauerhaften Fragmentierung des verbliebenen Waldes bei. Dies hat außerdem zur Folge, dass der Anteil an Waldränder dauerhaft erhöht wird. Tropische Bergwälder sind durch eine ausgeprägte Heterogenität von Lebensräumen gekennzeichnet, die in erster Linie auf Höhenlage und Topographie zurückzuführen sind. Zu diesen natürlichen Umweltgradienten kommen heute neue Stressgradienten, wie zum Beispiel Randeffekte. Studien zeigen, wie Höhenlagen und andere topographische Gegebenheiten die Zusammensetzung und die Struktur von Pflanzengesellschaften beeinflussen. Allerdings liegt ihr Schwerpunkt selten auf der Evaluierung der unterschiedlichen Komponenten funktioneller Diversität.

Abweichende Blattmerkmale, evolviert durch verschiedene Strategien zur Nutzung von Ressourcen, sind wichtige Indikatoren der Artenverteilung, da sie im engen Zusammenhang mit Umweltgradienten und Artenzusammensetzung stehen. So ist es hilfreich, Erkenntnisse über die funktionelle Diversität mit den Reaktionen der Pflanzengesellschaften auf natürliche und anthropogen induzierte Stressgradienten zu verbinden, um Mechanismen zu verstehen, die die Artenverteilung beeinflussen sowie auf potentielle Konsequenzen durch Umweltveränderungen hinweisen. Darüber hinaus zeigen weiterführende Studien, dass sich Randeffekte auch auf interspezifische Interaktionen auswirken, z.B. bei der Bestäubung und Samenausbreitung. In Anbetracht der großen

Bedeutung, welche diese Interaktionen auf den Genfluss von tropischen Arten haben, wäre zu erwarten, dass Randeffekte sich bis auf die genetische Struktur von Pflanzenarten auswirken können.

Ziel dieser Doktorarbeit ist es dazu beizutragen, den Einfluss von natürlichen Umweltgradienten und Randeffekte auf funktionelle Pflanzeneigenschaften und genetische Strukturen, mit Hilfe des Modellsystems Bergwald der bolivianischen Anden, zu verstehen. Die erste Studie untersuchte dabei die Beziehungen zwischen Umweltfaktoren und diversen Blattmerkmalen, die eine unterschiedliche Ressourcennutzung erlauben, sowie Unterschiede in der funktionellen Zusammensetzung und Struktur in Bezug auf Höhenlage, Topographie und Randeffekte. Es zeigte sich, dass Blattmerkmale stärker auf Bodeneigenschaften als auf das Mikroklima reagieren. Dies zeigt die Bedeutung des Bodens für die Veränderung der funktionellen Zusammensetzung dieser Wälder. Die Dominanz von Arten mit einer konservativen Strategie in stressreicheren Habitaten, wie z. B. hohen Lagen, Bergrücken und Waldrändern, zeigte die Bedeutung von Stress als Einflussfaktor auf funktionelle Merkmale und Artenverteilung. Die Ergebnisse warnen auch vor Effekten durch Umweltveränderungen, die durch Fragmentierung und Eingriffe durch Landnutzung in Ökosysteme entstehen, wie zum Beispiel Veränderungen im Nährstoffkreislauf, welche mit variierenden Blattmerkmalen in Zusammenhang stehen. Die Aufrechterhaltung von funktionellen Strukturen über Stressgradienten hinweg deutet darauf hin, dass weniger häufige Arten dazu dienen Stresseffekte abzumildern. Dies unterstreicht die Bedeutung der funktionellen Redundanz in artenreichen Gesellschaften.

Die zweite Studie untersuchte Randeffekte auf genetische sowie kleinräumliche, genetische Strukturen (SGS *spatial genetic structure*) von zwei durch Zoochorie verbreitete Arten. Die genetischen Unterschiede zwischen Populationen von *Clusia* *sphaerocarpa* and *Clusia lechleri* an Waldrändern und im Waldinneren unterstützen die Annahme, dass induzierte Umweltveränderungen, wie Randeffekte, auch auf kleiner räumlicher Skala zu genetischer Divergenz führen können. Dies verstärkt die Bedeutung von Habitatunterschieden für die genetische Differenzierung. Größere SGS im Waldinneren im Vergleich zu Waldrändern sind höchst wahrscheinlich auf erhöhte Samenverbreitung und Populationsgröße von *Clusia* Arten zurückzuführen, die an Waldrändern begünstigt werden und zeigt einen Break-up Lokale genetischen Strukturen.

Diese Doktorarbeit liefert neue Erkenntnisse über die Rolle der Fragmentierung in Bezug auf ihre Induzierung von Stressgradienten. Des Weiteren legt sie dessen Einfluss auf die funktionale Diversität und die genetische Struktur von Gehölzarten in tropischen Bergwäldern dar. Auswirkungen von Randeffekten können auf vielfältigen Ebenen der Artorganisation festgestellt werden; von der Verbreitung der Arten bis hinunter auf deren kleinräumige genetische Struktur. Diese weitreichenden Konsequenzen sollten bei zukünftigen Entscheidungen zur Landnutzung und Umweltschutzprogrammen mit einfließen.

RESUMEN

Cambios en el uso de la tierra y en consecuencia la fragmentación de hábitat, constituyen factores determinantes de cambio ambiental global. Debido al uso de fuego para obtener aéreas de cultivo mediante roza y quema, grandes aéreas de bosque montano tropical resultan altamente fragmentadas. Frecuentemente, quemas descontroladas se extienden al bosque contribuyendo así a una permanente configuración de bosque fragmentado con grandes áreas de borde. Así, la fragmentación de hábitat a través de los “efectos de borde”, podría considerarse un factor adicional de stress y cambios en las condiciones ambientales de estos bosques.

Los bosques montanos tropicales exhiben una gran intrínseca heterogeneidad ambiental, principalmente atribuida a la altitud y topografía. Previos estudios indican que la altitud y la topografía afectan la composición y estructura de comunidades vegetales, pero su rol como factores determinantes de cambios en diferentes componentes de diversidad funcional es menos conocido. Igualmente, poco se conoce acerca de los efectos de la fragmentación sobre la diversidad funcional de comunidades vegetales en bosque montano. Caracteres foliares, asociados al uso de recursos, determinan en gran parte el éxito de colonización y sobrevivencia de las plantas frente a gradientes medioambientales y constituyen importantes indicadores de distribución y ensamblaje de especies. En este sentido, información acerca de cambios en la diversidad funcional de las comunidades vegetales respecto a gradientes tanto de estrés natural como al inducido por la fragmentación, podrían esclarecer mecanismos de distribución de especies y advertir sobre consecuencias potenciales de cambios ambientales inducidos por la fragmentación. Asimismo, varios estudios sustentan efectos de borde sobre interacciones planta-animal, tales como la polinización y dispersión de semillas. En plantas tropicales, la influencia de estas interacciones en el flujo genético de sus poblaciones es altamente reconocida, por tanto, los efectos de borde podrían también extenderse sobre la estructura genética de sus poblaciones.

La presente tesis considera bosques montanos de los Andes bolivianos como sistema de estudio y tiene por objetivo evaluar como gradientes de stress, naturales (asociados a la elevación y topografía) e inducidos por el hombre (asociados a efectos de borde), afectan la diversidad funcional y estructura genética de especies leñosas. En el primer estudio se evalúa la relación entre variables medioambientales y caracteres foliares. Se evalúan también, variaciones en la composición y estructura funcional respecto a la elevación, topografía y efectos de borde. Los resultados indican que caracteres foliares asociados a estrategias de uso de recursos (conservativa o adquisitiva) responden a variables edáficas más que a variables micro-climáticas. Esto resalta la importancia del suelo como un factor determinante de cambios en la composición funcional de éstos bosques. La dominancia de especies con una estrategia conservativa en hábitats con mayor estrés, tales como hábitats situados a mayor altitud, en lomas y en bordes de bosque; muestra la importancia del estrés ambiental como factor determinante de variaciones en caracteres funcionales y distribución de especies. Considerando que los caracteres foliares evaluados están estrechamente relacionados con la descomposición y productividad de los bosques; los resultados de esta tesis también advierten acerca de posibles efectos de borde sobre el funcionamiento del ecosistema. Finalmente, una menor influencia de los gradientes de stress sobre la estructura funcional, sugieren un rol amortiguador de especies menos abundantes frente al stress ambiental y resaltan la importancia de la redundancia funcional en comunidades con alta riqueza de especies.

El segundo estudio evalúa los efectos de borde sobre la estructura genética y la estructura genética espacial local (fine-scale spatial genetic structure, SGS) de dos especies del genero *Clusia*, cuya polinización y dispersión de semillas es principalmente realizada por animales. Los resultados muestran diferenciación genética entre poblaciones de *Clusia sphaerocarpa* y *C. lechleri* situadas en borde e interior de bosque. Así, cambios en el ambiente inducidos por el hombre, tales como efectos de borde, pueden conducir a cambios en la divergencia genética de especies vegetales inclusive a una escala geográfica pequeña. Esto resalta la importancia de la diferenciación de hábitat como factor determinante para la diferenciación genética. Los resultados también muestran mayor SGS en áreas de interior de bosque en comparación con los bordes de bosque, lo que indica una ruptura en la estructura genética local de las poblaciones de *Clusia sphaerocarpa*. Esto se explica debido a un posible incremento en la dispersión de semillas y el tamaño poblacional de estas especies en áreas de bordes de bosque.

La presente tesis aporta información novedosa acerca del rol de la fragmentación como inductor de gradientes de estrés en bosques montanos tropicales y su impacto sobre la diversidad funcional y estructura genética de especies leñosas. Así, se muestra como los efectos de borde se extienden sobre múltiples niveles de organización, desde la distribución de especies a nivel de comunidad hasta la estructura genética espacial local (SGS) a nivel de población. Estas extensas consecuencias deberían ser consideradas en programas de conservación al momento de evaluar y tomar decisiones acerca de los impactos producidos por el cambio en el uso de la tierra.

CHAPTER

I

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Environmental gradients in tropical montane forest

Tropical montane forests harbour high species richness of vascular plants (Myers *et al.* 2000, Richter 2008) and are considered world hotspots of biodiversity (Myers 1988, Mittermeier *et al.* 1998). Their high species diversity is in part attributed to their high environmental heterogeneity because it leads to the co-existence of different vegetation types and favors ecological specialization (Richter 2008, Homeier *et al.* 2010). As part of this heterogeneity, elevation and topography, due to their intrinsic environmental gradients (Körner 2007, Bräuning *et al.* 2008), are recognized as important drivers to generate changes in plant species composition and forest structure (Lieberman *et al.* 1996, Takyu *et al.* 2002, Homeier *et al.* 2010). Stress is defined as external constraints limiting the rates of resource acquisition, growth or reproduction of organisms (Grime 1989), and may vary along these environmental gradients. It is thus considered an important driver of habitat structuring and can explain plant distribution and population dynamics (Trémolières 2004) as well as interactions between species (Maestre *et al.* 2009). Knowledge about how plant species and communities respond to gradients of stress turns helpful to predict and cope with the consequences of human induced changes on the environment.

Forest fragmentation and habitat loss become important environmental issues in the last decades (Laurance 1999). Although, tropical montane forests provide important ecosystem services, especially as water sources (Bruijnzeel & Proctor 1995, Hölscher *et al.* 2008), few is known about how fragmentation drives ecosystem functioning in these systems. Edge effects, defined as diverse physical and biotic alterations associated with the artificial boundaries of fragments (Ewers *et al.* 2007), constitute important drivers of environmental changes in fragmented landscapes (Murcia 1995, Laurance *et al.* 2007). Edge effects have shown serious impacts on species diversity and composition, community dynamics, ecosystem functioning and species interactions in tropical forests (Saunders *et al.* 1991, Aizen & Feinsinger, 1994, Vasconcelos & Luizão 2004, Lippok *et al.* 2013). As drivers of environmental changes and stress, they may also extend to effects on functional traits (Diaz & Cabido 2001) and genetic structure of tropical plant species. However, little information is found in the literature in this respect. Some studies report changes in plant functional traits within the context of fire-prone plant communities (Müller *et al*. 2007, Brando *et al*. 2012) or evaluated genetic variability (Ramos *et al.* 2010) within the context of forest edges, but almost nothing is found for tropical montane forests. Information about how plants species respond to stressed environments such as induced forest edges, would be important to induce natural regeneration or develop restoration projects in these forests.

Functional diversity and environmental gradients

Although evaluations of biodiversity are mainly based on species richness, nowadays more focus is given to functional traits as indicators of biodiversity responses to environment changes and effects on ecosystem functioning (Lavorel & Garnier 2002, Garnier *et al.* 2004, Diaz *et al.* 2007). Functional traits refer to characteristics of an organism, which are considered relevant to its response to the environment and/or its effects on ecosystem functioning (Diaz & Cabido 2001, Bello *et al.* 2010). Thus, functional diversity (FD) is defined as the value, range and relative abundance of organismic traits present in an ecosystem or community (Diaz & Cabido 2001). The environment, through filtering of traits showed to be an important driver of FD components related to functional strategies and species assemblages (Bello *et al.* 2012, Reich 2014).

Environmental factors such as resource availability and disturbances showed to affect plant response traits and therefore plant strategies (Grime *et al.* 1997, Lavorel & Garnier 2002, Ackerly 2004). The role of resource availability as a main driver of plant strategy selection (Aerts & Chapin 2000, Sandel *et al.* 2010) is reflected in the plant strategy axis "leaf economic spectrum" (Wright *et al.* 2004). This global pattern describes, through correlations among leaf traits, a trade-off between two different acquisitive strategies: a) quick returns of investment of nutrients and dry mass in leaves (i.e., high physiological rates, nutrient concentrations and low leaf mass per area) and b) a conservative strategy characterized by slow return, stress-tolerance and the opposite set of traits. Depending on their strategies, species will be differently distributed with respect to the type and degree of habitat stress i.e. fertility, water and light availability (Grime *et al.* 1997, Kühner & Kleyer 2008, Reich 2014). Shifts between strategies imply shifts in the presence and relative abundance of certain functional traits in the community, and therefore in the functional composition of communities (Díaz & Cabido 2001). Since further important properties of the ecosystem such as resilience and resistance are related with plants strategies (Lepš *et al.* 1982, Aerts 1995, MacGillivray *et al.* 1995), evaluations of functional composition turn relevant for taking adequate measures of management and conservation of ecosystems (Bernhardt-Römermann *et al.* 2011, Maeshiro *et al.* 2013).

Functional traits' responses to environmental constraints are also related with assembly rules (Belyea & Lancaster 1999, Bello *et al.* 2012). It is assumed that communities are composed by species with appropriated traits to reach and establish in circumstances set by the environment and other organisms (abiotic and biotic) (Keddy 1992, Belyea & Lancaster 1999). Thus, environment, through habitat filtering, would select individuals with specific traits to be either sorted out or persist in a community (Keddy 1992). This may lead to a convergence of traits because under particular environmental conditions, species with traits that permit to adapt better to the habitat will be more successful (Weiher & Keddy 1995, Cornwell & Ackerly 2009). Later, traits would be "filtered out" mainly by limiting similarity (Macarthur & Levins 1967), which results in a divergence of traits because groups of species with different traits would compete less, and therefore co-exist better (Kraft *et al.* 2008, Katabuchi *et al.* 2012). This trait variation in communities can be described by three primary components of functional diversity (functional richness, functional evenness and functional divergence) (Mason *et al.* 2005, Villéger *et al.* 2008) and these components have the potential to reveal assembly processes (Mason *et al*. 2012). They were also suggested as good indicators of effects of environmental changes on functional structure (Mouillot *et al.* 2013). Thus, knowledge about them contributes to the understanding of ecological processes related with assembly rules and also warns about consequences of induced human environmental changes (Paine *et al.* 2011, Pakeman 2011).

Up to now, information about patterns of functional diversity in tropical montane forests is mainly focused on elevation (Velázquez-Rosas *et al.* 2002, Read *et al*. 2013). On other factors, which involve environmental gradients like topography, information is scattered (Takyu *et al.* 2003, Deng *et al.* 2008) and evaluation of edge effects on functional diversity has not been previously reported. Environmental drivers like fragmentation, land use and climate change, which certainly induce new stressful environment for species, may affect FD patterns (Laliberté *et al.* 2010, May *et al.* 2013, Soudzilovskaia *et al*. 2013). Besides, recently more attention is being given to the role of functional traits as link between biodiversity and ecosystem processes, services and thus human well-being (Diaz & Cabido 2001, Garnier *et al*. 2004, Diaz *et al.* 2007). Highly diverse ecosystems as tropical mountain forest with high environmental heterogeneity certainly represent a challenge system for studying patterns of functional diversity. However, their immense importance as source of high biodiversity and ecosystem services, which at the same time are highly threatened by environmental human induced changes (Millennium Ecosystem Assessment

2005), increases the need of knowledge about responses of plant communities to natural and induced environmental changes.

Genetic structure and environmental gradients

Genetic differentiation was mainly studied under the concept of isolation by distance (Wright 1943), which assumes that increasing geographic distances will increase genetic differentiation among populations as a result of genetic drift and a reduction of gene flow through dispersal limitation. Nowadays, it is more recognized that changes in environmental conditions between geographically close populations may also increase genetic divergence (Shafer & Wolf 2013, Mallet *et al.* 2014). Ecological contrast and environmental dissimilarity among habitats can reduce the establishment success of immigrants in a receiving habitat, and thus reduce gene flow among populations (Orsini *et al.* 2013, Shafer & Wolf 2013).

Different factors like mating system, life form, seed dispersal and population density showed to be important determinants of fine-scale spatial genetic structure (SGS) (Vekemans & Hardy 2004, Hamrick & Trapnell 2011). SGS reflects the non-random distribution of genotypes in the environment and it is mainly attributed to seed dispersal limitation (Vekemans & Hardy 2004). Thus, a high value of SGS indicates that genetic relatedness between plants is high at short distances and that the progeny is dispersed in clumps or close to the maternal plant. Population density and seed dispersal distances have important influence on SGS because low population size and short seed dispersal distances may lead to little seed and gene shadow overlap, and therefore to high genetic relatedness of neighbouring plants (García & Grivet 2011). The contrary may lead to large seed and gene shadow overlap, increasing admixture of maternal genotypes and thus decreasing SGS (Hamrick *et al.* 1993, Hamrick & Trapnell 2011). Environmental gradients, which affect population sizes and species interactions, may therefore extend to changes in SGS of species.

Edge effects not only comprise changes in environmental conditions but they are also important determinants of changes in mating systems, seed removal, pollination and population size (Murcia 1995, Ewers *et al*. 2007, del Castillo *et al.* 2011). Gene flow via pollination and seed dispersal constitutes an important determinant of genetic diversity (Dick *et al.* 2008). In tropical plants, these processes are mainly mediated by animals (Jordano 2000, Ollerton *et al*. 2011). Although edge effects certainly constitute induced environmental gradients of stress and may extend to changes in plant-animal interactions (Ness 2004, Burgess *et al.* 2006, López-Barrera *et al*. 2007), few studies focus on their effects at the genetic level (Ramos *et al.* 2010, Tarazi *et al*. 2013). I used *Clusia sphaerocarpa* Planchon & Triana and *C. lechleri* Rusby (Clusiaceae) as study species to evaluate edge effects on their genetic structure. They are common trees in montane cloud forests of Bolivia (de Roca 1993) and are distributed both at edges and interior forests in the study area. Their pollination and seed dispersal is reported to be mediated mainly by animals (Gustafsson *et al*. 2007), so they constitute interesting and feasible species to evaluate edge effects on genetic structure and SGS (figure 1).

Figure 1 Morphological and reproductive characteristics of *Clusia sphaerocarpa* and *C. lechleri* (photos by A. Apaza). A) Tree of *C. lechleri*. B) Feminine flowers and C) masculine flowers of *C. sphaerocarpa*. D) Feminine flowers and E) masculine flowers of *C. lechleri*. F) Fruits of *C. lechleri*.

OBJECTIVES

In order to understand the influence of natural and human induced gradients of stress on functional diversity, I evaluated different aspects of FD at the community level with respect to elevation, topography and edge effects. Furthermore, I evaluate how human induced changes of the environment like edge effects may also extend to the genetic level affecting the genetic diversity and SGS of two sympatric species of *Clusia*.

The first study (**chapter 2**) evaluates relationship between environmental variables and leaf traits, changes in functional composition and functional structure across an elevational range of 600 m, from 1900-2200m asl, topography (ridge and gorges) and edge effects (forest edge and forest interior). In order to explore whether leaf traits respond to soil properties and microclimate variables in terms of plant resource-use strategy, we tested their relationships by the means of a fourth corner analysis. Subsequently, considering that stress increases in high elevations, edges and ridges, it was tested whether the functional composition (CWM = community weighted mean index) of leaf traits reflect a conservative strategy in these habitats and an acquisitive strategy in low elevation, interior forest and gorges. Finally, considering the same gradient of stress I evaluated changes in multidimensional functional diversity indices (FRic = functional richness; FEve = functional evenness; FDiv = functional divergence) to evaluate changes in functional structure.

The second study (**chapter 3**) evaluates changes in genetic variation, differentiation and SGS between areas at forest edges and forest interior in *Clusia sphaerocarpa* Planchon & Triana and *C. lechleri* Rusby (Clusiaceae). I evaluated changes in genetic diversity and genetic differentiation between populations in forest edges and forest interior and also small-scale genetic structure (SGS) between habitats and among age classes.

STUDY AREA

The study was carried out in the eastern cordillera of the Bolivian Andes surrounding the town of Chulumani (capital of South Yungas province). Two remaining forests with different sites for each chapter were chosen for the study (10° 20’ 50.60’’ S 67° 30’ 48.46’’ W) (16° 24’ 39.12’’ S 76° 34’ 00.91’’ W) (figure 2). Considering its vegetation, it corresponds to the “Yungas montane seasonal evergreen forest” (Mueller *et al.* 2002, Navarro 2011). The nearest climatic station indicates a mean annual precipitation of 1459 mm with drier months between April to September (Molina 2005) and a mean annual temperature of 20.8°C. As other regions in the tropical Andes (Myers *et al.* 2000, Mittermeier *et al*. 2011), Yungas Bolivian mountain forest corresponds to one of the hotspots of biodiversity and harbour high species richness of vascular plants (Kessler 2001). Besides, the region of South Yungas has a long ancestral history of coca (*Erythroxylon coca*) production and although agriculture was also based in production of citrus, nowadays coca crops are highly extended. One major threat for habitat loss and forest fragmentation in these forests is the traditional practice of "chaqueo". This practice uses fire to clear land and grow crops but often fires get out of control and spread to the forest. After their use, many areas are abandoned resulting in a configuration of patches of forest-grassland (Killeen *et al.* 2005) (figure 3). Due to their steep topography and loss of vegetation, tropical montane forests face the loss of important ecosystem services like maintenance of water resources and protection from landslides (Bruijnzeel & Proctor 1995). Thus, restoration projects represent an alternative for conservation of these forests.

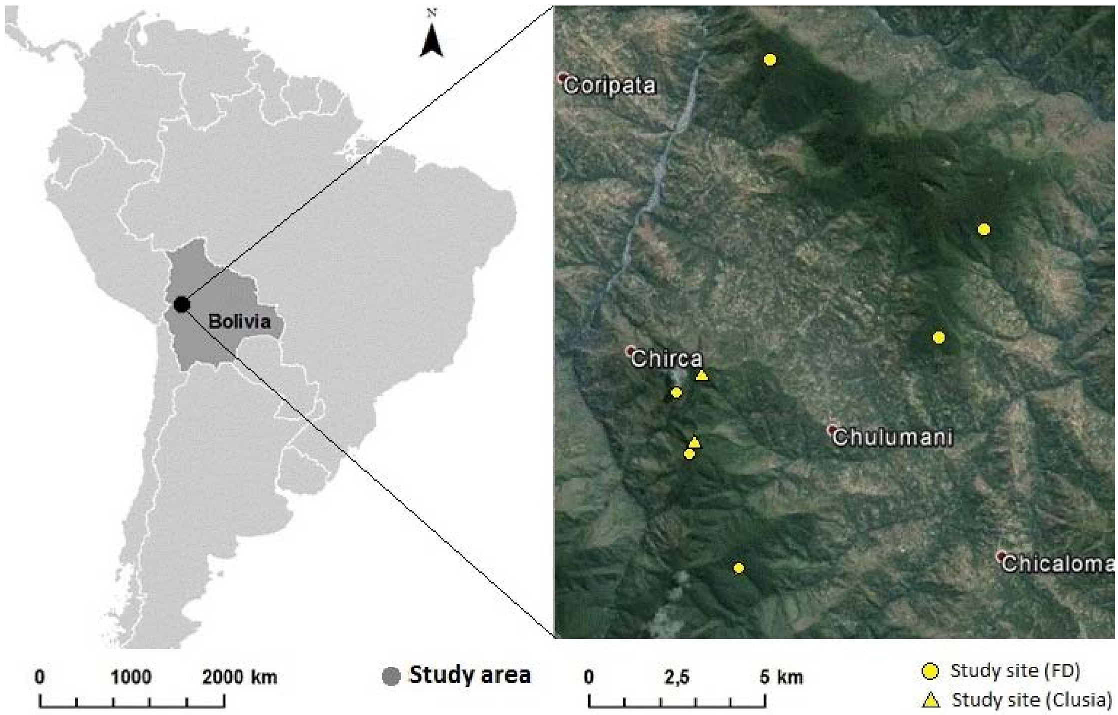

Figure 2 Map showing the study area and the sites where plots are distributed. FD = Sites for the Functional Diversity study. Clusia = Sites for the genetic study on *Clusia sphaeroarpa* and *C. lechleri*.

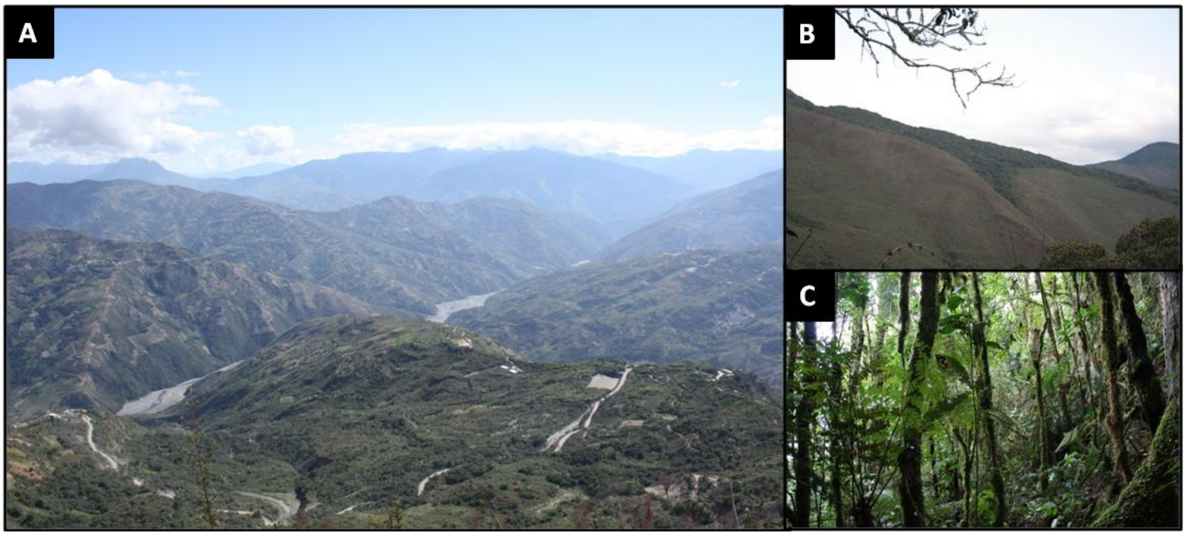

Figure 3 View of the study area (photos by A. Apaza). A) Deforested landscape in the South Yungas region in Bolivia. B) Edge forests result of the deforestation. C) Interior of the forest in the fragments.

CHAPTER

II

Natural and Human-Induced Environmental Gradients Drive Functional Composition of Woody Plant Species in Tropical Montane Forests

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Matthias Schleuning and Sabine Both

(Biotropica, under review)

ABSTRACT

Environmental gradients play a major role driving plant communities. How natural and human induced environmental gradients are associated with leaf traits and to what extent they drive functional composition and structure is poorly understood for tropical montane forests. In a species-rich tropical montane forest in Bolivia, we studied associations of soil properties and microclimate with six leaf traits related to resource use, measured on 119 woody plant species. We considered stress gradients associated with elevation (from 1900 m to 2500 m asl), topography (ridge and gorge) and edge effects (forest edge vs. forest interior). We evaluated changes in functional composition, measured by community-weighted means (CWM), and functional structure with multidimensional functional diversity indices (FRic, FEve and FDiv) across these gradients. Fourth-corner analysis revealed associations between leaf traits and soil properties in accordance with the trade-off in resource use strategy between acquisition and conservation of resources. Functional composition shifted from the dominance of acquisitive species in habitats at low altitudes, gorges and forest interior to dominance of conservative species in habitats at high altitudes, ridges and forest edges. Functional structure was only affected by topography, with higher values of FRic in ridges compared to gorges. We show the importance of soil properties and environmental gradients for driving functional composition of woody plant species in relation to plants' resource-use strategies. Weak effects of all environmental gradients on the functional structure of the plant communities are in line with high species turnover in these forests and enhance the importance of their high species richness.

Keywords: Acquisitive-conservative trade-off; Bolivia; environmental gradients, fourth corner analysis; fragmentation; functional diversity; leaf traits; topography; tropical montane forest.

CHAPTER

III

FOREST FRAGMENTATION AND EDGE EFFECTS ON THE GENETIC STRUCTURE OF *Clusia sphaerocarpa* AND *C. lechleri* (Clusiaceae) IN TROPICAL MONTANE FORESTS

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ABSTRACT

Fragmentation of tropical forests influences abiotic and biotic processes that affect the genetic structure of plant populations. In forest fragments, edge effects, i.e. changes of abiotic and biotic factors at forest edges, may be prevalent. In two forest fragments (c. 200 ha at c. 2450 m asl) of tropical montane forest in Bolivia, sympatric populations of the dioecious tree species *Clusia sphaerocarpa* and *C. lechleri* were used as case study species to compare genetic diversity and small-scale genetic structure (SGS) between edge and interior habitats. Eight microsatellite markers were employed to genotype 343 individuals including adults, juveniles and seedlings of *C. sphaerocarpa* and 196 of *C. lechleri*. Genetic differentiation was found between habitats in both species (Φ_{RT} = 0.071 for *C. sphaerocarpa* and Φ_{RT} = 0.028 for *C. lechleri*) and among ages in *C. sphaerocarpa* (Φ_{RT} = 0.016). Overall, SGS was weak but significant with more pronounced SGS in *C. lechleri* (*Sp* = 0.0128) than in *C. sphaerocarpa* (*Sp* = 0.0073). However, positive spatial genetic autocorrelation extended only up to 10 m. For *C. sphaerocarpa*, SGS was stronger in seedling and juvenile stages than in adults and in the forest interior than at forest edges. Our results show that edge effects can extend to the genetic level by breaking-up local genetic structures, probably due to increased gene flow and enhanced pollination and seed-dispersal interactions at forest edges.

Keywords: *Clusia*, edge effects, genetic differentiation, montane forest, SGS

CHAPTER

IV

SYNTHESIS

GENERAL DISCUSSION

Environmental gradients are considered important determinants of global diversity patterns in plant ecology (O'Brien *et al.* 2000, Qian 2013). It is thus crucial to quantify and understand how functional traits respond to environmental gradients in order to assess potential reactions of biodiversity to global environmental changes (McGill *et al.* 2006). Associations between leaf traits and soil properties support the importance of environment as a filter of traits in woody species in our study area and thus their importance for shaping plant communities as well (Keddy 1992). In accordance with McIntyre *et al.* (1995), this thesis also supports that stress gradients affect trait composition in plant communities. Changes in CWM were responsive to natural and induced gradients of stress changing community plant strategies related with resource-use leaf traits. Thus, it is verified that the major axis of the fundamental trade-off between acquisition and conservation of resources (Diaz *et al.* 2004, Wright *et al.* 2004) also applies for tropical montane forests. Finally, changes in genetic structure of *Clusia* species related to edge effects show the importance of induced environmental gradients in tropical montane forest also at the genetic level.

This thesis emphasizes the importance of soil nitrogen as driver of resource economic strategies of leaf traits for tropical montane forests. Previous studies have shown that soil is a crucial determinant of habitat filtering and drives the distribution of plant traits in other species-rich plant communities (Katabuchi *et al.* 2012). Soil nitrogen was previously recognized as an important determinant of species composition in tropical mountain forests (Tanner & Kapos 1982, Tanner *et al.* 1998) and its availability is positively related with net primary productivity (Gruber & Galloway 2008, LeBauer & Treseder 2008). It is also reported that species with conservative leaf traits (Wright *et al.* 2004) lead to low decomposition rates, therefore changes in functional composition as a result of land use change also affect the decomposition process (Bakker *et al.* 2011). Litter decomposition is considered a key ecosystem process for nutrient cycling and an important component of the global carbon budget (Aerts 1997, Didham 1998, Bakker *et al.* 2011). Considering these aspects, the dominance of species with a conservative strategy adapted to areas with low fertility would also be favoured in eroded soils resulting from fragmentation or certain land use types. This may involve important consequences for the nutrient and carbon cycling of tropical montane forests. Information about litter decomposition would be useful for understanding better the effects of fragmentation on nutrient cycle processes and for taking adequate measures of soil management in the montane forests of Bolivia.

Despite the responses of functional composition to stress gradients this study did not find changes in functional structure. These stronger effects of stress on mean communities' traits than on trait variation may indicate a degree of functional redundancy in the responses of species to stress. Similarly, in another study in tropical forest that evaluated land use effects on functional diversity, changes in functional structure were not as evident as in functional composition (Carreño-Rocabado *et al.* 2012). The role of less abundant species to promote functional redundancy during environmental perturbation is considered important for ecosystem resilience (Naeem 1998). Thus, species-rich forests are assumed to have high resilience because the less abundant species may act as buffer for disturbances in the ecosystem (Walker *et al.* 1999, Lyons *et al.* 2005). Tropical montane forests with high environmental heterogeneity may favour communities with more plasticity to respond to the natural environmental changes. They may thus, need this resilience as buffer for natural disturbances and stress. Since land-use as an important driver of environmental change, has been shown to reduce functional redundancy (Laliberté *et al.* 2010), fragmentation and edge effects may also affect resilience of these forests. Consequently, studies that evaluate the role of less abundant species in tropical montane forests may elucidate mechanisms related with resilience and thus clarify the weak effects of environmental gradients on functional structure.

As showed, environment has an important role filtering traits, therefore determining species distribution in tropical montane forests. The genetic study on *C. lechlerii* and *C. sphaerocarpa* supports that habitats with contrasting stress gradients as edges and interior forests also determine changes in genetic differentiation and SGS. Environmental gradients determine genetic differentiation a) indirectly through changes in ecological interactions as seed dispersal and pollination, which determine gene flow, as well as b) through changes in the habitat suitability for establishment of differentially adapted seedlings (Orsini *et al.* 2013, Shafer & Wolf 2013). This thesis supports that contrasting environments at close geographic distances lead to genetic divergence (Orsini *et al.* 2013, Mallet *et al.* 2014). Since isolation by environment is consider a driver of ecological speciation (Shafer & Wolf 2013), this finding highlights the importance of environmental heterogeneity in tropical montane forests with regard to their high species richness (Richter 2008, Homeier *et al.* 2010). Recently, dispersal and biotic interactions are considered important factors that limit the range of plant species distribution (Boulangeat *et al.* 2012). Dispersal limitation may prevent species to reach suitable sites outside of their current distribution, but also to reach unsuitable sites and exhibit source-sink dynamics (Pulliam 2000). Plant-animal interactions (Gallegos *et al.* 2014), as well as pollinator composition (Kambach *et al*. 2012) responded to environmental changes as part of edge effects in the study area of this thesis. Moreover high species turnover is reported across natural and induced gradients of stress (Lippok *et al.* 2013). Thus, the role of natural environmental gradients in tropical montane forest for promoting different levels of genetic differentiation remains to be evaluated. Future evaluations relating functional traits and genetic patterns may help on one hand to understand, basic concepts of the dynamic and assembly of species related with the high biodiversity in tropical montane forest, and, on the other hand, to prevent threats of human induced changes in the environment.

This thesis also addresses the issue of edge effects as anthropogenically induced change of environmental conditions and its role as stress driver in this ecosystem. Few is known with respect to vegetation responses to edge effects in tropical mountain forest and most of the studies focused on effects on composition, structure and interactions of species (Restrepo *et al.* 1999, Cayuela *et al.* 2009, Lippok *et al.* 2013). As shown before, changes in the composition of traits in the community have important implications for plant communities. Increases in the dominance of conservative strategies at edges may possibly have effects on ecosystem processes as for example decreasing productivity (Chapin *et al.* 2003), reducing the rate of decomposition (Cornwell *et al.* 2008, Bakker *et al.* 2011) or increasing the risk of fire (de Magalhães & Schwilk 2012). Considering that montane forests in Bolivia are highly affected by human induced fires, information about plant flammability traits would be relevant in future studies. Similar, edge effects on the genetic level as found for *Clusia* species, promoting genetic differentiation and decreasing SGS at edges, can also be expected for other species. Effects in the genetic structure of *Clusia* species, which are characterized by a conservative strategy (Lüttge & Duarte 2007) and favoured in stressed habitats, may change for species with more acquisitive traits, whose populations are less adapted to the environmental stress at forest edges. For the latter species, possibly a reduction in population size may drive responses with opposite direction than in species with more conservative traits like *Clusia* species. Furthermore, investigations of reproductive traits and regeneration are necessary to identify strategies related to secondary succession and may also help to predict genetic and FD responses to edge effects.

Similarly to other mountain forest in the northern Andes (Etter & Wyngaarden 2000), the region of South Yungas in Bolivia is highly affected by fragmentation since centuries because it constitutes a traditional area for coca production. Forest edges are an important part of its configuration and should be considered in conservation programs. Nowadays, fragmentation is increasing and new measures for the conservation of the forest like restoration would be an alternative. In that case, evaluations of functional diversity are suggested as an important component for monitoring restoration programs. They help identifying efficient methods for program implementation and give information about the ecosystem services that are aimed to return (Cadotte *et al.* 2011, D'Astous *et al.* 2013). The importance of maintaining genetic diversity to enhance ecosystem services in restoration projects is also suggested (Reynolds *et al.* 2012). Thus, in order to apply successful measures of conservation in these forests, information about their function and species responses to stress are important for implementing and monitoring future restoration programs.

CONCLUSIONS

This thesis showed that natural and induced gradients of stress drive functional trait composition and that the respective edge effects also extend to the genetic level. Thus, it contributes to the better understanding of the role of environmental heterogeneity of tropical mountain forest as driver for species composition at the community level and for genetic structure at the population level. At the same time it warns about effects of induced human changes in the environment as result of fragmentation. The importance of soil properties as driver of functional composition is highlighted and consequently also possible effects of fragmentation at the level of ecosystem functioning. This thesis constitutes pioneer work to assess integrative studies of functional diversity on tropical montane forest in Bolivia and shows its importance as a new focus for evaluating biodiversity.

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LIST OF PUBLICATIONS

Publications of this dissertation

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ERKLÄRUNG ÜBER DEN PERSÖNLIHEN ANTEIL AN DEN PUBLIKATIONEN

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Unterschrift:..............................

EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Stress gradients - drivers of functional diversity and genetic patterns of woody species in tropical montane forest (Bolivia), a link to edge effects" 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.

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