Stand diversification and tropical ecosystems: community ecology of beetles and ecosystem functioning in Sardinilla, Panama

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August 2017

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science.

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Abstract

Deforestation is a growing threat to biodiversity in the tropics. In the last few years, a number of reforestation initiatives, such as agroforestry systems, have been put in place. However, agroforestry systems are under threat by herbivory and this influence can be felt even at a very small scale. In fact, herbivores can have highly disproportionate effects on tree functioning. This research focuses on the role of stand diversification in reducing insect herbivory damage, using the Sardinilla plantation as a model site. The research will improve our understanding of the role played by herbivores in regulating processes in the ecosystem.

Chapter 1 establishes the context of the research, focusing primarily on reviewing scientific knowledge about insect herbivory and ecosystem functioning as well as the effect of stand diversification on ecosystem resilience. Chapter 2 describes and characterizes the beetle community in the Sardinilla plantation, Panama, in relation to stand diversification and local environmental variables. Our results show that experimental manipulation of tree diversity impact overall beetle community assemblages, for both morphospecies and functional diversity, and that the beetle communities in diverse tree stands are functionally even. Additionally, canopy openness and vegetation, which regulates microclimate, has a significant effect on beetle communities. Chapter 3 focuses on using Structural Equation Modeling (SEM) to assess relationships between environmental variables and beetles in an experimental neotropical agroforestry setting. The major findings of this exploratory analysis show that there is a negative relationship between aboveground biomass and beetle diversity and between beetle diversity and herbivory. Aboveground plant biomass also seemed to be the most important determinant of herbivory.

This thesis establishes links between herbivory and ecosystem functioning in the Sardinilla plantation. Moving forward, the information gathered will contribute to the wealth of knowledge already accumulated by the Sardinilla project during the last 15 years. Understanding the potential effects of herbivores in agroforestry systems is a step towards ensuring the sustainability of these forests and support their use as an initiative to counter deforestation in Central America.

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Résumé

La déforestation cause de plus en plus d'inquiétude pour la conservation de la biodiversité dans les tropiques. Durant les dernières années, plusieurs initiatives de reforestation ont été mises en place, telles que l'implantation de systèmes agroforestiers. Pourtant, ces systèmes font face à plusieurs menaces, et ce, même à une petite échelle. En effet, les herbivores peuvent avoir un effet disproportionné sur le fonctionnement des arbres, surtout en comparaison à leur petite taille. Ce mémoire même l'emphase sur le rôle du taux de diversification des arbres sur la réduction des dommages causés par les herbivores et utilise la plantation de Sardinilla (Panama) comme site modèle. Cette recherche pourra améliorer notre compréhension du rôle joué par les herbivores dans la régulation des processus écosystémiques.

Le Chapitre 1 établit le contexte de la recherche, en se concentrant sur une revue de la littérature scientifique sur les insectes herbivores et le fonctionnement des écosystèmes, mais aussi sur l'effet du taux de diversification sur la résilience des écosystèmes. Le Chapitre 2 décrit et caractérise la communauté de coléoptères dans la plantation de Sardinilla, en relation avec le taux de diversification, ainsi que certaines variables environnementales locales. Nos résultats démontrent l'impact général de la diversification sur l'assemblage des communautés, autant au niveau des morpho espèces qu'au niveau fonctionnel, en plus d'être uniformes en termes de diversité fonctionnelle. De plus, l'ouverture de la canopée et la couverture végétale, qui régulent le microclimat, ont un effet significatif sur les communautés de coléoptères. Le Chapitre 3 utilise la modélisation par équation structurelle (SEM) pour évaluer les relations liant les variables environnementales aux coléoptères dans ce système agroforestier tropical et expérimental. Les principaux constats de cette analyse exploratoire montrent une relation négative entre la biomasse aérienne et la diversité des coléoptères et entre la diversité des coléoptères et les taux d'herbivores. De plus, la biomasse aérienne semble être le facteur décisif sur le niveau d'herbivores.

Ce mémoire établit des liens entre les herbivores et le fonctionnement de l'écosystème dans la plantation de Sardinilla. En allant de l'avant, les informations

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amassées contribueront au bagage de connaissances accumulées par le projet Sardinilla depuis 15 ans. Comprendre les effets potentiels des herbivores sur les systèmes agroforestiers est un pas vers la gestion durable de ces forêts et supporte leur utilisation comme initiatives pour contrer la déforestation en Amérique centrale.

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Thesis Format

This thesis is presented in manuscript style and is organized into a series of chapters. Chapters 2 and 3 will be later submitted to scientific journals in ecology and entomology. Chapter 1 is a literature review which provides background information surrounding the topics introduced in the following two chapters and also acts to introduce the thesis rationale as well as the specific research questions and objectives.

Acknowledgments

I would first like to thank my supervisor Chris Buddle, for his insight, constructive criticism, guidance and support during the past few years. I would especially like to thank him for his understanding of those of us struggling with mental health issues through grad school. It means the world to have this kind of support. Thank you to my co-supervisor Don Windsor for his help and guidance during my stay in Panama. I also have to thank my lab mates (Shaun Turney, Elyssa) Cameron, Gail MacInnis, Jessica Turgeon and Chris Cloutier) who have helped me throughout the whole project, through statistical expertise, revision, edits and perspectives. I am grateful that our lab cultivates an atmosphere of mutual support and openness, not only academically, but on a personal level too. An immense thank to Lady Mancilla and José Monteza for their help coordinating the field work in Sardinilla and to Catherine Potvin for allowing me to conduct my research in the research plantation. I would also like to thank Andrew McLennan for his meticulous work with my voucher specimens. Finally, a big thank you to my friends, especially my roommate and best friend Camille and family for their love and support. Also, a special thank you to all the wonderful cafés in Rosemont for their soothing work atmosphere and great coffee that fueled the writing of this thesis. Financial support was provided by McGill University from BESS-CREATE grant as well as Graduate Excellence Awards, the Margaret DuPorte Fellowship and by the National Science and Engineering Research Council of Canada (NSERC) (Discovery Grant and Northern Research Supplement to Christopher Buddle).

Contribution of Authors:

I wrote all the original manuscripts and literature review in this thesis. I also collected all the data and performed the data analyses. Both supervisors, Christopher Buddle (McGill University) and Donald Windsor (Smithsonian Tropical Research Institute), appear as co-authors due to their contributions in the conceptual design, feedback and editing of the manuscripts.

Catherine Potvin (McGill University) will be a co-author in the published articles due to the data contributions from the Sardinilla database as it is in large part a result of research using her funding sources. Marina Duarte, a PhD student in Catherine Potvin's lab, will also be a co-author in the published article for Chapter 3 as she agreed to share part of her data for my research. Finally, Hector Barrios (Universidad de Panama), who provided guidance during the identification process, will be a co-author in Chapter 2.

Details of the contributions of many others are outlined in the acknowledgments section of each chapter.

Chapter 1: Introduction and Literature Review

1.1 Introduction

1.1.1 Thesis rationale

Reforestation is now considered an important development tool for rural communities in Latin American countries and is increasingly used as a tool for regeneration of the soil and plant communities in degraded areas (Plath et al. 2011). Tree diversity experimental plantations, which investigate the relationships between tree diversity and composition and their effect on biogeochemistry and other ecosystem processes, can help us understand the implication of plantations on ecosystem health. The Sardinilla project, located in the Sardinilla plantation near Buena Vista, in the province of Colón, Panama, investigates the effects of stand diversification on ecosystem functioning, including carbon and nitrogen cycling, and water table levels.

In experimental plantations, herbivores have potentially damaging effects on the trees. Insect herbivores, defined here as insects that feed on plant tissues, are especially important in tropical ecosystems since they make up the majority of primary consumers (Novotny and Basset 2005; Novotny et al. 2012). It is hypothesized that stand diversification, increase in tree diversity in a forest stand, may lessen the negative impacts of herbivory (Plath et al. 2011; Plath et al. 2012), but this may vary depending on the host specificity of insects (Plath et al. 2011). Mixed stands of native tree species have also been shown to have positive effects on the ecosystem such as improved nutrient cycling (of carbon and nitrogen), increased soil fertility and increased overall biodiversity of the stand (Plath et al. 2011). Diversity can also be incorporated into agroforestry in order to protect against risks of fluctuating environmental conditions and to regulate the abundance of undesirable organisms (Altieri 1999; Hooper et al. 2005). Thus, the presence of higher diversity in agroforestry ecosystems can help enhance the sustainability of the plantation.

In the context of reforestation initiatives in Central America, and in Panama in particular, understanding the impacts of herbivory can help improve the delivery of ecosystem services by those forests (Hambäck and Beckerman 2003; Butler, Vickery, and Norris 2007; Tylianakis, Tscharntke, and Lewis 2007). Understanding how insects interact with the rest of the forest ecosystem can help by providing a more holistic way of describing the ecosystem and the processes taking place. Insect herbivores make up most of the primary consumers in neotropical forests and can inhibit the successful establishment of forest plantations. Still, the identity of the taxa responsible for most of these plant-herbivore interactions are almost unknown to date (Strauss and Zangerl 2002; FAO 2009). It is therefore imperative to identify such interactions, which can then inform management decisions (Garen et al. 2009) and optimal plantation design to minimize effects of herbivory. This project will provide information on the development of plantations with native species in a mixed stand to promote reforestation in tropical regions and on the secure economical livelihood of the population depending on harvesting such plantations (Bhagwat et al. 2008; Chazdon et al. 2009).

1.1.2 Research objectives

The overarching goal of this thesis is to explore the interrelations between beetle herbivore diversity, community structure, and ecosystem functioning, and how all three variables respond to stand diversification in an agroforestry context in the neotropics. This research focuses on the role of stand diversification as a tool to lessen herbivory damage, and the Sardinilla plantation in Panama is used as a model site for this. The research will help improve our understanding of the role played by herbivores in regulating processes in the ecosystem.

Chapter 1 establishes the context of the research, focusing primarily on reviewing scientific knowledge about insect herbivory and ecosystem functioning as well as the effect of stand diversification on ecosystem resilience. Chapter 2 is a data chapter and it specifically examines the effect of stand diversification and local environmental variables on beetle assemblages, both at the morphospecies and

functional level. This chapter focuses on describing the communities in the Sardinilla plantation. Chapter 3 explores the causal relationships in the Sardinilla system using Structural Equation Modeling, with a goal of providing recommendations about how to understand the mechanisms behind ecosystem functioning in tropical timber plantations.

The specific objectives of this thesis are:

Chapter 1: The objective of this chapter is to review the literature and provide background information on reforestation initiatives and plantations in Central America. It will also examine the interactions between insect herbivores and ecosystem processes such as nutrient cycling and temperature regulation. Finally, it will review previous findings on the use of stand diversification to increase ecosystem stability and resilience to pests.

Chapter 2: The primary objective of this chapter is to describe communities of beetles (Coleoptera) in the Sardinilla plantation. This chapter will test the effect of stand diversification on beetle diversity and community structure. It will also investigate the patterns of functional diversity in the different groups, and explore the effects of key environmental variables on beetle communities.

Chapter 3: The primary objective of this chapter is to explore links between herbivory and ecosystem functioning variables using Structural Equation Modeling. The goal is to test a theoretical model of the plantation in order to highlight areas that should be considered for future research.

Chapter 4: The final chapter will summarize the entire thesis and provide some recommendations for future research in insect herbivory and ecosystem functioning in tropical agroecosystems.

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1.2 Literature Review

This literature review will provide some background to the thesis, including: agroforestry in the neotropics, beetle diversity, and the effects of beetle diversity on ecosystem functioning. I will look at these topics through the lens of the implementation of mixed species plantations in sustainable agroforestry systems.

1.2.1 Reforestation plantations in Central America

The widespread deforestation problem in Panama and Central America

One of the highest rates of deforestation in the tropics has been observed in Latin America. The situation in Panama and in neighbouring countries has been deteriorating for several decades (FAO 2011). Despite the important and widely-recognized roles of tropical forests in carbon sequestration and other ecosystem services, deforestation continues (FAO 2006). Conversion of land to pasture resulted in extensive grazing and changes in the ecosystem functioning (Wassenaar et al. 2007). This type of conversion also affects short-term ecosystem carbon budgets by increasing inter and intra-annual variations in ecosystem CO2 fluxes (Priante-Filho and Vourlitis 2004; Randow, Manzi, and Kruijt 2004; Saleska, Rocha, and Kruijt 2009). Tropical forests, especially mature ones, provide us with multiple other ecosystem services such as hydrology, local climate regulation and timber production (Hall et al. 2011). However, some researchers have suggested that some of those services could be obtained from naturally regenerating forests or plantations (Lamb, Erskine, and Parrotta 2005; Oliver and Mesznik 2006; Chazdon 2008; J. Benayas et al. 2009).

Reforestation Initiatives

Some of the main drivers of forest plantation initiatives are the expanding demands for not only bioenergy (such as using wood as fuel; Energy 2007), but also for carbon markets (FAO 2011; Sprenger et al. 2013). While tree plantations are rapidly increasing (FRA 2005), most of them consist of monocultures and often use the same small pool of exotic species (Parrotta 1999; Binkley et al. 2003; Nichols, Bristow, and Vanclay 2006). The use of native species for reforestation and restoration is becoming a more appealing alternative. They provide ecosystem services at a higher rate than exotic species (Butterfield 1995; Montagnini, Gonzalez, and Porras 1995), including soil stabilization, reduced erosion, seed deposition, habitat for several animals and increased understory diversity (Wishnie et al. 2007). The spread of monocultures of exotic species can endanger local plant biodiversity. This biodiversity is essential in maintaining ecosystem resilience and the biogeochemical processes that it needs (Healey and Gara 2003). Thus, the establishment of mixed-species plantations has received more attention from both scientists and government officials (Loreau et al. 2001; Assessment 2005). It is not enough to plant trees to regenerate ecosystems, but to plant the right trees for the given situation.

Mixed plantations can result in better land use, improved access of trees to nutritional resources and reduced impact of insect or pest damage. Surprisingly, there is also a possibility for financial gains by using with a mix of slow- and fast-growing species. With these combinations, it is possible to harvest fast-growing species earlier, in rotation with longer growing species, which are often more valuable (Redondo-Brenes and Montagnini 2006). This strategy can provide a more continuous cash flow, as well as improved growing conditions for longer-lived species (Lamb and Gilmour 2003). Fast-growing species can, however, decrease water availability at the ecosystem level (Malmer et al. 2010), which is a particular concern with the increase of drought in Panama in the past few years (McNutt 2014).

Plantations of mixed species, and especially native species, are not widespread since they are considered harder to manage and harvest. One of the main reasons is that it is hard to find species that will cohabit well together and will maintain some stability while having some commercial success. Since this practice is not common, there is a lack of studies able to predict successful species combinations (Lamb and Gilmour 2003; Forrester, Bauhus, and Cowie 2005; Kanowski and Catterall 2005). Fortunately, several studies have started to explore this issue and

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have determined that above ground biomass and carbon sequestration in mixed native species plantations are comparable to monoculture plantations. Therefore, the mixed native tree species are able to cohabit (Montagnini and Porras 1998; Stanley and Montagnini 1999). Additionally, some mixed plantations using native species are starting to be implemented successfully for reforestation in the tropics (Redondo-Brenes and Montagnini 2006; Weber et al. 2008), although the benefits promised by mixed native tree plantations on ecosystem functioning have yet to be fully demonstrated (Oelmann et al. 2010).

In addition to helping ecosystem recovery, the afforestation of pastures is considered an effective measure to sequester carbon. Afforestation is a way of regenerating agricultural lands by reducing excess production in agriculture, increasing the production of wood and other forest products, improving environmental performance of the land, and promoting integrated multi-purpose rural land use planning (Gilliams et al. 2005). Such initiatives could mitigate increasing CO₂ concentrations (FAO 2009) and lessen the effects of the original deforestation. Malhi, Meir, and Brown (2002) estimated that such efforts in tropical regions could provide a mitigation potential of 15% of global CO₂ emissions. These measures could also be encouraged further in coming years with international carbon accounting of the Kyoto protocol (Wolf, Eugster, Potvin, and Buchmann 2011; Wolf, Eugster, Potvin, Turner et al. 2011) and especially in Panama with carbon credit initiatives (CentralAmericaData.com 2012).

While it seems obvious to convert pastures back to forests to improve carbon sequestration, the socio-economic situation in Central America makes it difficult to do. Many rural communities depend on small-scale agriculture and use land that has been deforested and converted to pastures. These communities are especially vulnerable to deteriorating agricultural conditions, including declines in soil, water and other resources health (Altieri 1995). There is necessarily a trade-off between the conservation and regeneration of biodiversity and the resources and livelihood of rural communities (Altieri 1999).

1.2.2 Herbivory and ecosystem functioning

Herbivory, in this thesis, is defined as feeding on plant tissues from all parts of the tree. Although other animals may be herbivorous (e.g., browsing ungulates), the focus for this thesis is on insect herbivores. The effect of herbivory diversity on ecosystem functioning is not necessarily directly correlated with changes in abundance or richness of surrounding tree species. Since all tree species do not fill the same niche or some have an especially dominant effect on the ecosystem, increasing diversity will not always change the rates of processes (Hooper et al. 2005). Additionally, the overlap of resource use by different tree species can affect the stability of those processes. Because of niche partitioning, an increase in functional richness could lead to better use of resources and greater total productivity of the ecosystem. However, this will not necessarily translate into higher productivity in silvicultural terms (Paine et al. 2015). Because research has shown that tree species differ in how they acquire, store, and recycle nutrients (Cuevas and Lugo 1998; Forrester et al. 2006), we can assume that they will also differ in how they react to disturbances such as herbivory damage. These speciesspecific traits can then influence ecological processes immensely (Healy, Gotelli, and Potvin 2008).

Nutrient Cycling and Productivity

A surprising aspect of insect herbivory in forest ecosystems is the dual effect it can have on its surroundings. While there are negative effects on plant productivity due to biomass removal, the positive effect on nutrient cycling might outweigh it in some contexts (Hartley and Jones 2004). Dyer, Turner, and Seastedt (1993) argue that there is a biphasic community response, meaning that at low levels of herbivory plant communities show an increase in productivity, but extreme herbivory causes a reduction in productivity. Additionally, the transition depends on both temporal and spatial variation as well as carbon and nitrogen availability (Holland and Detling 1990; Silva, Espirito-Santo, and Melo 2012). However, they also argue that herbivory has a stronger effect on ecosystem functioning in the context of longterm dynamics than at a shorter time scale (Huntly 1991). Therefore, it is preferable to investigate the effect of herbivory in long-term studies.

Decomposition

Herbivores, with different types of deposits (excreta, bodies, molts, unconsumed leaf fragments), are responsible for some of the litter production and will therefore affect subsequent decomposition (Metcalfe et al. 2014). Decomposition is a key process for carbon and nutrient cycling in forest and agroforestry ecosystems (Swift, Heal, and Anderson 1979). The rates of decomposition can be influenced by physico-chemical properties, as well as by the composition of soil organisms and microclimate conditions (Scherer-Lorenzen, Bonilla, and Potvin 2007). Variables influencing microclimate might affect both decomposition itself, but also the community of herbivores present.

The palatability of leaves to generalist herbivores will also affect decomposition rates. Since the higher the levels of tannins and phenolic compounds are, the lower the level of herbivory will be, insect herbivory may lead to an increase in of levels of phenolics and tannins in leaves as a defense by the tree. The quality of these high-phenolic and high-tannin plants is lesser and this could potentially affect decomposition rates (Hartley and Jones 2004). Litter production and decomposition are key processes in carbon and nutrient cycling (Scherer-Lorenzen, Bonilla, and Potvin 2007). Therefore, gaining information on another aspect of this process, such as herbivory, can help us better understand ecosystem functioning.

Photosynthesis

Most herbivory damage (around 75%) occurs on leaves before full expansion (Coley and Barone 1996). Since trees will compete for light, they will abscise damaged young leaves, even if the damage is not overt, because of their reduced photosynthetic rates (Blundell and Peart 2000; Hartley and Jones 2004). While the removal of these leaves might increase the photosynthetic rate of remaining

leaves, insect herbivory which does not involve the loss of plant tissue (such as damage caused by gallers, stem borer and phloem feeders) will decrease overall photosynthetic rates (Huntly 1991). Additionally, deciduous species (which are drought-avoiding in tropical ecosystems) will optimize their growth and photosynthesis rates during the rainy season. This strategy, as well as the varying phenology that it promotes, result in seasonal changes in the resource-use efficiency of deciduous trees (Sobrado 1991; Eamus and Prior 2001). The loss of photosynthetic leaf area as a result of herbivory might be detrimental in terms of plant carbon uptake and metabolic costs associated with repairing damage (Metcalfe et al. 2014). Finally, in a forest-wide perspective, Mattson and Addy (1975) concluded that the impact of insect herbivore will depend on the intensity of the defoliation, the quantity and distribution of photosynthetic biomass, and variable environmental conditions.

Drivers of Herbivory

Since young leaves have higher water content, nitrogen, protein levels, as well as lower phenolic compounds, their leaf damage increments are also higher (Silva, Espirito-Santo, and Morais 2015). As leaves mature, leaf nitrogen content is reduced and is replaced by a carbon-based compound, making the remaining leaves less edible for herbivores (Silva, Espirito-Santo, and Morais 2015). This mechanism indicates a temporal change in leaf traits and herbivory with leaf age (Boege and Marquis 2005; Silva, Espirito-Santo, and Melo 2012).

Since beetles are small-bodied and ectotherms, they have lower energetic requirements and faster gut passage times. These characteristics will result in lower foliar resource use (Parra 1978; Coley and Barone 1996). Metcalfe et al. (2014) showed that hole:leaf area ratio remained constant with leaf expansion. This is consistent with small invertebrates acting as herbivores. There is substantial research that shows that most of the leaf area loss in tropical forests is caused directly or indirectly by leaf chewing herbivores (García-Guzmán and Dirzo 2004; Ribeiro and Basset 2007).

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While defoliation can cause some damage, it rarely results in high mortality rates as the woody structure remains intact. Mortality can occur after repeated severe defoliation in a relatively short amount of time. When trees are not killed, the canopy will usually recover in weeks (Lovett et al. 2002). Therefore, while defoliation weakens the tree, it is not thought to be fatal. In the context of timber species, defoliation is not the type of damage that is most detrimental.

1.2.3. Stand diversification and ecosystem resilience

Biological diversity is considered an indicator of ecosystem resilience as it is associated with functional redundancy in key ecological processes (Folke et al. 2004; Dymond et al. 2014). While diversity is not the only component of resilience, it ensures buffering from variability in the productivity or health of the system (Yachi and Loreau 1999). Because most of the processes are heavily impacted by biotic actors, their maintenance will rely on the presence of biological diversity (Altieri 1999). Because of the variability of environmental conditions, even at a small scale, an assemblage made up of species with differing environmental sensitivities should have greater ecosystem stability. The redundancy acts as an insurance that allows ecological processes to continue despite species loss. Since species' responses to environmental changes vary both temporally and demographically, the probability is high in a diverse ecosystem that at least one species will be able to fill the functional role of a lost species (Hooper et al. 2005).

Resilience of Plant Communities

Differences in species composition have a strong effect on productivity. Therefore, community composition is as important for productivity as species or functional richness (Hooper et al. 2005). The diversity and abundance of traits in a community (Mouillot, Villéger, and Scherer-Lorenzen 2011) will affect ecosystem functioning, mostly because of niche differences between the species (Hooper et al. 2005). While the continuum of stand diversification has received some attention from researchers (Koricheva et al. 2006; Kunert et al. 2012; Setiawan et al. 2014), most

studies to date have focused on the difference between monocultures and mixtures, without focusing on a particular composition or diversity. The mixed plots in these studies are characterized by species with different traits in relation to resource acquisition. It is thought that the trait diversity will lead to complementary resource use and explain higher productivity and biomass in those stands compared to pure stands (Hector 1998). In the Sardinilla plantation, the previous conditions are fulfilled and resource use by the different tree species is complementary (Scherer-Lorenzen, Bonilla, and Potvin 2007; Oelmann et al. 2010).

Huntly (1991) claims that the amount of herbivory on a particular plant will depend on the local species composition by associational resistance. This form of indirect mutualism essentially decreases the number of individual types of herbivores per plant by increasing functional diversity. Another way in which local species composition may affect herbivory is that diverse stands tend to harbor more natural enemies of herbivores as well as attracting herbivores to alternative food plants. The different growing strategies present in the different tree species reflect both their successional roles and their functional roles in the plantation. Plants that are considered pioneer species will grow faster and replace tissues and damage faster than the slowest-growing ones. They will also differ in their chemical defenses and herbivory rates (Silva, Espirito-Santo, and Melo 2012). Therefore, the functional identity of the trees will be translated in the influence of species composition on ecosystem functioning.

Neotropical Beetles

Beetles (Coleoptera) are among the most diverse animals on the planet, and this is especially true in tropical regions (Erwin 1982; Erwin 1983). While there are many other herbivorous insects, herbivorous beetles are diverse in their strategies and functional roles in tropical ecosystems. Beetles occupy virtually all ecological niches, and even within herbivory, beetles exhibit a vast array of life history strategies including chewing, mining, rolling, galling, piercing and sucking

(Vehviläinen, Koricheva, and Ruohomäki 2007; Labandeira and Wilf 2007). Herbivore damage is often located on the leaves, which might have implication for the photosynthesis potential of the trees. Therefore, it affects the carbon cycling carried out by the trees, their growth (tree height and diameter) and their herbaceous productivity (Aide and Zimmerman 1990). However, herbivores can also attack other parts of the tree, such as flowers, fruits, roots and bark, all of which potentially impair the tree's reproductive success and fitness. Beetles are an ideal taxon for research on biodiversity and community ecology: while there is incredible diversity in the tropics, beetles as a taxon have been quite well studied, both taxonomical and ecologically. For the scope of this project, this group is well suited as it is both functionally diverse and logistically manageable.

Resilience of Beetle Communities

In temperate agroecosystems, if the primary plant host of a specialized herbivore is cultivated as part of a mixed stand, then the abundance of the specialist will be reduced compared to a monoculture of the host plant (Altieri 1999). The mechanisms behind this phenomenon act in two ways: by supporting natural enemies and by directly inhibiting pest attacks (Altieri 1999). Ideally, agroecosystems would be diverse and remain undisturbed, allowing more internal links to develop and promoting greater insect community stability. The different trophic levels will be stabilized and the perturbation in response to changes at the lower trophic levels will be minimal (Altieri 1999). However, the problem that monocultures pose might not necessarily be because of the simple composition, but because of the uniformly aged structure of the stand (Watt 1992), which makes it more vulnerable to attacks. Furthermore, the pattern of herbivore density follows a different pattern than their natural enemies. There is a lag in the predation rates compared to herbivore density, with predation rates being lower at the beginning of the rainy season, followed later by an increase. Herbivore density, in contrast, increases with the onset of the rainy season, peaks after 2 months and then tapers off until the end of the rainy season (Silva, Espirito-Santo, and Melo 2012).

In their meta-analysis, Jactel and Brockerhoff (2007) argued that tree diversity reduces insect herbivory in forest ecosystems. While the Sardinilla plantation is different from typical naturally-occurring rainforest in Panama, their conclusions can still inform us on the general trends that should be present in the plantation. In diverse plant communities, each particular species is less abundant, leading it to be less available to specialist herbivores (Kareiva 1983; Yamamura 2002). Since specialist herbivores are most often responsible for outbreaks, which can be extremely detrimental to tree survival, stand diversification is a good strategy to reduce herbivory damage. At the same time, polyphagous (generalist) herbivores do not cause more herbivory in mixed than in pure stands (Jactel and Brockerhoff 2007). These observations at Sardinilla are consistent with other research in tropical forests (Barone 1998; Barone 2000).

Stand diversification, while promoting a more stable and even insect community, will also confer redundancy at the ecosystem level. If the species used are functionally similar, but with different environmental sensitivity, ecosystem processes will be stabilized and will promote good growing conditions for the plantation as a whole (Ewers et al. 2015). In the context of reforestation initiatives in Central America, and in Panama in particular, understanding the impacts of herbivory can help improve the delivery of ecosystem services by those forests (Hambäck and Beckerman 2003; Butler, Vickery, and Norris 2007; Tylianakis, Tscharntke, and Lewis 2007). Understanding how insects interact with the rest of the forest can provide a more holistic way of describing the ecosystem and the processes that take place. Therefore, it is imperative to identify such interactions, which can then inform management decisions (Garen et al. 2009) and optimal plantation design to minimize effects of herbivory. This project will provide information for the development of plantations with native species in a mixed stand to promote reforestation in tropical regions, and secure economical livelihoods of the population depending on harvesting these plantations (Bhagwat et al. 2008; Chazdon et al. 2009).

1.3 References

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Connecting Statement

This chapter provided the context and background information for the research presented in the subsequent chapters. It outlined the objectives of the thesis and introduced the specific questions which will be addressed in Chapters 2 and 3. Chapter 2 is centered on the effect of stand diversification on beetle diversity and community structure. It will also investigate the patterns of diversity of the different functional groups, and explore the effects of key environmental variables on beetle communities.

Chapter 2: The effects of stand diversification on neotropical beetle assemblages

2.1 Abstract

Forests in the neotropics are home to an immense number of species and are essential for the conservation of biodiversity. The implementation of sustainable agroforestry as a mean of afforestation and ecosystem stabilization is regarded as a viable initiative. However, herbivorous insects can jeopardize the establishment and sustainability of such plantations. For this study, I described communities of beetles in the Sardinilla plantation, in terms of dominant species and functional groups. Most importantly, I tested the effect of stand diversification on beetle diversity and community structure and on the diversity of functional groups, as well as the effects of key local environmental variables on beetle communities. By sampling 21 plots of varying tree diversity treatments (1, 3, 6, 9 and 18 species), I caught 1850 beetles, from 43 families, 235 species and belonging to 16 functional groups. NMDS ordinations revealed that beetle assemblages were distinct and that the structure was driven by canopy openness and vegetation cover at the plot level. At the species level, treatment was significant in structuring beetle communities. However, at the functional level, treatments overlapped greatly, suggesting functional redundancy in the plantation, even in low diversity treatments. These results were corroborated by the relative abundance analysis showing high levels of evenness. Together, these results suggest high resilience of native tree assemblages to beetle herbivory. Additionally, few of the focal tree species influenced the structure of the beetle communities. Hura crepitans and Tabebuia rosea in particular drove the community composition. Anacardium excelsum, by its foliar extent was also a contributing factor of the insect community composition. This result suggests the importance of tree community composition as well as richness in lessening the harmfulness of herbivory in tropical agroforestry systems.

2.2 Introduction

Conservation of biodiversity in the tropics relies most importantly on the protection of species-rich areas. Neotropical forests are a good example of that as they harbour a colossal number of species. These species, plant and animal, interact with their environment providing ecological functions to the ecosystem. With deforestation being an important issue in Central America, the implementation of sustainable agroforestry as a mean of reforestation and ecosystem stabilization has gained a lot of attention. Sustainable agroforestry is defined here as the sustainable development of degraded lands whereby human activity is maintained and natural resources are conserved (Retnowati 2003). In addition to being beneficial for vegetation restoration, tropical agroforestry can act as a refuge for biodiversity by attracting neighbouring species (Driscoll and Weir 2005; Bhagwat et al. 2008).

We are conditioned to imagine forest degradation at large scales, with deforestation and turnover to agricultural lands being so prevalent. Yet some of the threats that forests face operate at much smaller scales. Herbivores, defined here as insects that feed on plant tissues, can have effects disproportionate to their actual size in terms of their influence on the tree functioning. Insect, and especially beetle, diversity plays an important role in agroforestry ecosystems. Many species, when they aggregate, can cause serious problems to these systems (Murgas, Barrios, and Luna 2009). Insects are especially important in tropical ecosystems seeing as they constitute the majority of the primary consumers and show high levels of host specificity. While leaf-miner damage is only restricted to a few tissues in the leaves, defoliators cause early leaf abscission, which can influence the photosynthetic potential of the trees (Aide 1993). Damage can also occur in several parts of the plant from chewing, mining, rolling, galling, piercing, sucking and leaf abscission (Vehviläinen, Koricheva, and Ruohomäki 2007; Labandeira and Wilf 2007).

Stand diversification, in which multiple tree species are planted in one region, may lessen negative impacts of herbivory (Plath et al. 2011; Plath, Dorn, Riedel, et al. 2012). Different theories have been used to explain this including chemical defenses (Tahvanainen and Root 1972; Finch and Collier 2000), host plant density (Root 1973), availability of nutrients (Lau et al. 2008), host plant quality (Mody, Unsicker, and Linsenmair 2007; Wise and Abrahamson 2007), natural enemy diversity and abundance (Root 1973) and tree species composition (Jactel and Brockerhoff 2007). However, reduction of herbivory by stand diversification may vary depending on the insect host specificity (Plath et al. 2011).

Even though insect herbivores comprise most of the primary consumers in the neotropical forest and can inhibit the successful establishment of forest plantations, the identity of the species responsible for most plant-herbivore interactions are largely unknown (Strauss and Zangerl 2002; FAO 2009). Therefore, it is imperative to identify such interactions to ensure more informed management decisions such as the use of broad-spectrum pesticides (Garen et al. 2009) and optimal plantation design to minimize effects of herbivory. The information could contribute to knowledge on the development of plantations using native species in a mixed stand. These plantations would then promote reforestation in tropical regions and secure economical livelihoods of the population depending on harvesting such plantations (Bhagwat et al. 2008; Chazdon et al. 2009).

Beetles (Coleoptera) are among the most diverse taxon on the planet (Erwin 1983), and are known as key herbivores in the neotropics (Lewinsohn, Novotny, and Basset 2005). They occupy virtually all niches as herbivores, from seed eaters to leaf chewers. Beetles are therefore an appropriate model taxon to test the relationship among herbivory, stand diversification and ecosystem function. There exists a large body of knowledge about the taxonomy and ecology of beetles in the tropics (work by Novotny, Basset, Barrios and Windsor). Novotny and Basset (2005), for example, identified herbivore guilds for several insect orders in the

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tropics. Other taxa such as Lepidoptera also play an important part in herbivory. Yet, the abundance and diversity of Coleoptera in the tropics and their potential for herbivory outbreaks in both native and exotic plantations (Nair 2001) justifies the study of their effect on the functioning of the ecosystems in which they occur.

While species level diversity is often used in community ecology, there is an increasing use of functional diversity in biodiversity studies (McGill et al. 2006). We can argue that functional diversity might have a higher influence on ecosystem functioning (Deraison et al. 2015). Since traits are what interact with the ecosystem and not species per say, they will affect ecosystem functioning in a more direct way (Hooper et al. 2005; Mouillot, Villéger, and Scherer-Lorenzen 2011). The use of functional diversity can help bridge the taxonomic impediment, especially in ecology studies, and reduce the number of people hours consumed by identification (Fountain-Jones, Baker, and Jordan 2015).

For this study, our objectives are to describe communities of beetles in the Sardinilla plantation, a stand diversification, agroforestry experiment in Panama, in terms of dominant species and functional groups. Most importantly, I aim to test the effect of stand diversification on beetle diversity and community structure and on the diversity of the different functional groups. We also investigate the influence of stand diversification on community composition between the different plots. Additionally, I am testing the effects of key local environmental variables on beetle communities.

2.3 Methods

2.3.1 Study site

The study was conducted in the Sardinilla plantation located in Sardinilla in the Buena Vista region of central Panama (9 °19'30" N, 79 °38'00 " W), approximately 20 km from Barro Colorado Island (BCI). The climate is semi-humid tropical with a mean annual temperature of 25.2 °C, a mean annual precipitation of approximately

2200 mm and a pronounced dry season from January to April (Scherer-Lorenzen, Bonilla, and Potvin 2007).

The plantation is dedicated to understanding the complex links between ecosystem biogeochemical cycling (especially C cycling), land use, and biodiversity in tropical environments over a long-term scale. This experimental site is designed to explore structural diversity of successional communities in a seminatural way and, especially, to develop sustainable agroecosystems in the Neotropics. The plantation relies on native tree species from Central Panama and models its species composition on the nearby island of Barro Colorado (BCI). The land, covering around 6 ha, was clear cut in 1953, cultivated for a few years and then used for cattle grazing for several decades. In 2001, the experimental plantation was established, with the use of six native tree species: two pioneers, Luehea seemanii (LS) and Cordia alliodora (CA), two light intermediate species, Anacardium excelsum (AE) and Hura crepitans (HC) and two long-lived pioneers, Cedrela odorata (CO) and Tabebuia rosea (TR). Twenty-four diversity plots were planted: six 6-species and six 3-species plots as well as 12 monocultures (Scherer-Lorenzen, Bonilla, and Potvin 2007), where the treatments were randomly assigned. The undergrowth is cleared annually to mitigate competition and facilitate work in the plantation. Species were selected based on their ability to grow in harsh conditions, economic or ecological importance and rates of growth on BCI. All these characteristics are shared with tree species that would promote sustainable establishment of reforestation initiatives. For this study, I selected 5 monoculture plots (Figure 2.1), one for each focal species except for Cordia alliodora since most specimens died during the first season, 5 of the three-species plot and 5 of the six-species plot, at random. Additionally, a second plantation was established in 2002 with treatments of six, nine or 18 species. For this plantation, I selected two of each tree diversity treatment, since there were only two of the blocks had the same compositional structure as the low diversity plantation.

2.3.2 Environmental variables

Several environmental variables were collected on site and were obtained from the Sardinilla database (Daniel Lesieur, UQAM), such as leaf-mass area (LMA), elevation, slope and moisture content. During the sampling period, I recorded vegetation cover (plants, grasses and shrubs) in each of the sampled plots and characterized it as follows: very sparse (<25%), sparse (25%-50%), dense (50%-75%) and very dense (75%-100%). Average height of the grasses and shrubs was also surveyed during the sampling season. I also calculated canopy openness using the GLA software (Frazer and Canham 1999) from hemispheric photographs taken in the summer of 2016.

2.3.3 Collection and identification

Specimens were collected between May and July 2016 using different sampling methods, both adapted to beetle collection. Flight intercept traps (Peck and Davies 1980), a passive sampling method, were placed in the middle of each of the sampled plots and were left out for a week to collect. We then reset the traps every week, for a total of seven weeks. As an active sampling method, I sampled using a beat sheet (Deutscher, Dillon, and McKinnon 2003), choosing three individual trees from each of the represented species in that plot at random. All branches were sampled up to 5m, and each branch was beat 5 times. Beetles that were present on the trunk and branches were also collected. Beat sheet sampling was done every two weeks for a total of five sampling events. Upon servicing a trap, I rinsed all samples with water, then placed them in a whirl pack and immersed them in 70% ethanol. All samples were taken back to the laboratory for processing.

All samples were sorted and separated into two categories: Coleoptera and non-Coleoptera. All Coleoptera were first identified to the family level, using several taxonomical references (e.g. Goode 1980; Arnett et al. 2002; Barney, Clark, and Riley 2009; Jiménez-Sánchez and Juárez-Gaytán 2015) and with the help of taxonomic experts. Specimens were identified to the genus when possible and classified into morpho species. To then classify specimens by function, genera (and species names when available) were used to search the literature for information on feeding habits of the specimens in tropical ecosystems (Appendix 2.1). The taxa were then classified into one of the following functional categories: rhizophagous (Ri), coprophagous (Co), phytophagous (Phy), mycophagous (Myc), necrophagous (Nec), predators (Pr), seed-eaters (Sd), bark borers (Bk), pollinators/flower feeder (Poll/FI), epiphyte feeders (Ep), litter feeders (Lt), xylophagous (Xy), frugivore (Fr), wood borers (Wd) and unknowns. Vouchers were made for each species, and are deposited at the Museo de Invertebrados Fairchild of the Universidad de Panama (Panama City, Panama) and at Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Canada).

2.3.4 Statistical analyses

We first tested overall diversity of the community based on morpho species and functional diversity. Rarefaction curves were constructed to determine if adequate sampling had been conducted (Buddle et al. 2005). These were created using the **rarefy** function from the **vegan** package (Oksanen, Blanchet, and Kindt 2011). All sampling periods were pooled. Since the morpho species rank abundance plot is quite skewed, the data was log transformed for all future analysis.

Next, I focused on assessing the effects of stand diversification on the overall abundance and diversity. Using the community data, I computed relative abundance and various diversity indices using the **vegan** package (Oksanen, Blanchet, and Kindt 2011). These indices were chosen to get a more complete picture of the trends in diversity. Trends in total relative abundance, morpho species and functional diversity (using multiple indices: Species richness, Simpson, Pielou's Evenness and Fisher's alpha) were tested using ANOVA's for an effect of treatment and dominant tree species. In order to visualize the community structure, especially the dominant taxa and functional groups, I produced rank abundance plots using the **rankabundance** function in the **BiodiversityR** package (Kindt 2012) in R 3.1.1 (R Development Core Team 2015) both for morpho species and functional groups.

To answer one of our main questions about the effects of stand diversification on beetle assemblages, I compared the differences in functional community composition between the different treatments. I calculated the relative proportions of the total abundance, for each treatment (pooled samples and sampling periods), and for the functional roles.

I used NMDS ordinations with a Bray-Curtis community matrix to test similarities between plots and between treatments at different taxonomic (family and genus) and functional scales using the metaMDS function in the vegan package of R (Oksanen, Blanchet, and Kindt 2011). The matrices were log transformed to account for skewed distribution of sampling. Ordinations allowed us to visually represent community similarity in a multidimensional space where each point represents a beetle assemblage from the different plots. I then used PerMANOVA to determine the influence of treatment, environmental variables, leaf attributes and tree abundance on beetle community structure. All temporal replicates were pooled since some taxa have extremely narrow emergence windows and the interest of the study was on the beetle community over the course of the entire season rather than the change through time. Environmental variables (canopy openness, vegetation cover, etc.) were plotted on the ordination space as vectors, using the envfit function in vegan (Oksanen, Blanchet, and Kindt 2011) and I determined their influence on community composition. These vectors were tested for a significant effect in shaping the observed communities. To generate statistical values for each habitat, centroids were determined using the ordispider function and 68% confidence intervals were added using the ordiellipse function (Oksanen, Blanchet, and Kindt 2011).

2.4 Results

2.4.1 Beetle Diversity and Abundance

Over the course of the project, 1850 beetles were collected, from 43 families and 235 morpho species all comprising 16 functional groups. Chrysomelidae (leaf

beetles) was the most abundant family (595 specimens) and contained the two most dominant morpho species: *Rhadopterus* sp. 2 and *Syphrea* sp. 1. Chrysomelidae was followed by Staphylinidae (305 specimens) and Scarabaeidae (119 specimens). Chrysomelidae was also the most diverse family. When comparing species by their rank abundance (Fig. 2.2a), few morpho species were highly abundant while most morpho species were present in low abundance. For functional groups (Fig. 2.2b), herbivores were the most dominant group (35.23% of the total abundance) and this is fitting with the species level findings. Predator and coprophagous beetles followed, making up 21.86% and 7.7% of the total number of specimens respectively. However, in terms of adequate sampling of the plantation, taxon sampling curves reached an asymptote for functional groups, but not for species, and that was apparent when looking at the curves for all treatments (Fig. 2.3 a and b). Therefore, I only considered functional groups when testing for richness in the ecosystem, using both functional richness and other common biodiversity indices.

At the functional level, while treatments were not significant for any of the biodiversity indices using ANOVA, the identity of the dominant tree species in the different plots was significant both when using Simpson's index (p=0.543, Table 2.3) and Pielou's evenness (p=0.004739, Table 2.3).

2.4.2 Community Structure

Focusing on relative abundance, overall functional richness seemed to increase with tree diversity (Fig. 2.4). While most functional groups were present in all treatments, their proportion changed depending on the tree diversity treatment. While predaceous beetles were dominant in monocultures, their proportion decreased with tree diversity treatment. In contrast, the proportion of generalist herbivores increased with tree diversity, with their highest proportion coinciding with the highest tree diversity. Herbivorous beetles generally followed that distribution, but peaked at the central tree diversity, 6 species (Figure 2.4). All the other groups increased in proportion with increasing tree diversity, suggesting an

increase in functional diversity with increasing stand diversification. When using PerMANOVA to the NMDS ordination, treatment was deemed significant in explaining both species (p=0.006, Table 2.1) and functional group composition (p=0.037, Table 2.2). However, when looking at particular biodiversity indices (Table 2.3), none of them significantly explained the difference in community composition in relation to increasing tree diversity in the treatments.

2.4.3 Environment Variables

Using NMDS ordination, I determined that beetle morpho species assemblages were oriented along microhabitat gradients mostly driven by canopy openness (p=0.001, Table 2.1) and to a lesser extent by soil vegetation cover (p=0.064, Table 2.1). While there was some overlap, the different tree diversity treatments clustered along this gradient, which seemed to follow the direction of canopy openness in the ordination space. All other tested environmental variables (soil moisture, slope, ambient temperature, etc.) had no effect on overall beetle assemblages. However, variables pertaining to tree identify and abundance and leaf attributes were significant in determining the community composition. The LMA values for *Anacardium excelsum* (p=0.001, Table 2.1) and the abundance of *Anacardium excelsum* (p=0.091, Table 2.1), *Tabebuia rosea* (p=0.010, Table 2.1), *Lueha semannii* (p=0.008, Table 2.1) and *Hura crepitans* (p=0.007, Table 2.1) were all significant or very close too.

On the other hand, at the functional level, beetle assemblages were mostly driven by canopy openness (p=0.045, Table 2.2) and not significantly by soil vegetation cover (p=0.207, Table 2.2). The disposition of the plots in the ordination space was different than for the morpho species level ordination. Additionally, there was a higher amount of overlap when looking at the tree diversity treatment clusters. As with the species level, all other tested environmental variables had no effect on the assemblages. In terms of tree identity variables, the LMA values for *Anacardium excelsum* (p=0.042, Table 2.2) and the abundance of *Hura crepitans* (p=0.032, Table 2.2) and *Tabebuia rosea* (p=0.028, Table 2.2) were significant.

2.5 Discussion

The objective of this research was to describe and characterize the beetle community in the Sardinilla plantation, Panama, in relation to stand diversification and local environmental variables. Our main results show that herbivores dominate the Sardinilla beetle community and that stand diversification treatment impact overall community assemblages, for both morpho species diversity and functional diversity. Additionally, canopy openness and vegetation, which regulates microclimate, has a significant effect on beetle communities.

2.5.1 Beetle Diversity and Abundance

It was expected that herbivores would be dominant based on the results from other studies focusing on beetles in the Sardinilla plantation, according to sampling period and time of the year (Plath and Barrios, unpublished data; Barrios 2003). While this dominance is a general pattern in beetle diversity (Whitfeld et al. 2012), it can also be explained by the amount of resources present in the plantation compared to the surrounding agricultural landscape (Audino, Louzada, and Comita 2014). The plantation in Sardinilla is surrounded by pastures and cattle ranching land, where tree biomass is very low. While the Sardinilla plantation is less dense than natural forests, it contains a great number of resources than the surrounding area, which will attract subsequent diversity (Wise and Abrahamson 2007). The plant biomass of those trees will therefore be able to support many herbivores, as the data showed. However, the results showed that, while herbivores were dominant, they were not occupying the same niche in each of the plots and their functional roles were more finely partitioned, especially as tree diversity in the plots increased.

Rare species dominated the beetle assemblage at Sardinilla. As seen in the rank abundance (Fig. 2.1), there is a high number of singletons or doubletons, meaning species that are present respectively only 1 or 2 times, in the samples. While this rarity is a pattern often observed in nature, especially for insects and especially in

the tropics (Missa et al. 2009), this situation could also be caused by the high occurrences of "tourists" or transient species passing through the plantation. Therefore, the traps could have picked up individuals that do not reside in the plantation, and probably biased our conclusions. The small physical extent of the plantation suggests that this is a probable source of variation. However, there are other possible reasons for the presence of such high numbers of rare species. Especially in the tropics, niche specialization plays a big role in insect communities (Novotny and Basset 2000). Even in large sampling events, the singletons often represent more than half of the species collected (Morse, Stork, and Lawton 1988; Basset and Kitching 1991; Novotný 1993). Under-sampling will also account for this pattern and both will be interconnected to explain the large amount of rare species. Some sampling methods are more adequate for either generalist or specialist species and will therefore skew the sample. It is also extremely hard, especially in the tropics to sample adequately, even with mass collecting methods (which could not be used in this case) (Lewinsohn, Novotny, and Basset 2005). Inadequate seasonal sampling is also a problem since I may not have captured the full phenology of some species (Janzen 1988; Erwin 1995; Novotny and Basset 2000).

2.5.2 Community structure

This research emphasized the importance of the diversity of beetle function, especially in the tropics. This functional diversity has incredible ecological importance and will affect local communities through their role in the food web (Lassau et al. 2005). These roles are reflected in their foraging behaviours (Lawrence and Britton 1994) as mentioned earlier. The use of functional diversity in ecological studies has increased in recent years, especially in studies investigating ecosystem functioning and biological diversity in the light of restoration and reforestation programs (Díaz and Cabido 2001; Mouchet, Villéger, and Mason 2010; Cadotte, Carscadden, and Mirotchnick 2011; Brudvig 2011). In highly diverse tropical ecosystems, choosing a group of organisms to act as bioindicators (i.e. taxa that indicate environmental conditions (Gerlach, Samways,

and Pryke 2013)) can alleviate some of the collection burden and help us reach ecological conclusions more easily. Beetles are often used for these types of studies because of their incredibly diverse function and sensitivity to ecosystem changes. They also utilize a variety of resources and respond fairly quickly to changes in ecosystem functioning. As an order, beetles encompass a much more diverse functional niche than any other insect order. Additionally, while a lot is still unknown, the taxonomy and ecology of this taxon is fairly well known. Together, they provide a set of ecological functions on which we can infer the health of a particular ecosystem (Audino, Louzada, and Comita 2014).

Figure 2.4 highlights the importance of such diversity, not only in the tropics, but especially in agroforestry systems. The latter is especially noteworthy. Indeed, while we should not dismiss species level diversity, functional diversity is more interesting in this case. In the context of sustainable agroforestry systems, the good functioning of the ecosystem has a higher influence on the survival of the plantation that biodiversity alone (Spehn and Gessner 2006).

By comparing the functional and morpho species ordination (Fig. 2.5) and the relative abundance plot (Fig. 2.4), I can conclude that, while the communities differed in terms of species composition, there is a functional redundancy within and between the treatments. I assume this is due to the high degree of overlap in functional groups, suggesting all functions are represented across the entire plantation, independent of the stand type. It is generally accepted that diversity creates redundancy to the ecosystem. While this is true for plant communities and can provide resilience to pest attacks, this is also true with insect communities (Thébault and Fontaine 2010). This redundancy provides stability in the face of disturbance (Ewers et al. 2015). This may confer a certain resilience of the insect community in the whole plantation, and even in the monoculture plots. The presence of most functional groups in the high diversity plots, as well as the higher proportion of generalist species suggests that herbivore pressure is not overwhelming to the timber species (Jactel and Brockerhoff 2007). Combined with

the higher evenness in the higher diversity plots, there may be an equilibrium between the consumers and their predators. An interesting aspect of the ANOVA analysis is the relationship between stand diversification and evenness in the functional groups. Evenness seemed to increase with tree diversity, showing that stand diversification promoted similar abundance in all functional groups. This is in accordance with our results from the relative abundance analysis and fits with data obtained from other studies. Fonseca and Ganade (2001) found that assemblages with higher functional evenness presented more functional redundancy since species were more evenly distributed among the different functional groups. These results support our hypothesis that higher stand diversification will have a positive effect on beetle functional diversity and will promote a gain in response diversity (variability of responses to disturbances among species that contribute similarly to ecosystem function) (Elmqvist, Folke, and Nyström 2009; Laliberté and Legendre 2010; Audino, Louzada, and Comita 2014).

The ratio of specialist to generalist herbivores is also noteworthy. There is a general pattern which shows that the diversity of species, and especially of specialists, will increase as the forest community more closely resemble the "natural" forest (Audino, Louzada, and Comita 2014). In this case, this translates into higher tree diversity treatments. However, the overall proportion of specialists in terms of abundance does not increase. In fact, it is the abundance of generalists that increases. Our result from Figure 2.4 corroborates the relationships observed in other tropical ecosystems (Barone 1998; Barone 2000), as it shows that increasing tree diversity promotes higher abundance of generalists. In mixed stands, the overall herbivory by polyphagous beetles is not expected to be higher than in monocultures. Oligophagous beetles, which are specialist herbivores, will exert higher herbivory pressure on their system (Jactel and Brockerhoff 2007). However, our results show that specialist abundance decreased with increasing stand diversification, leaving more space for generalists, especially generalist herbivores.

How different groups respond to disturbances may help explain this result. In plantations such as Sardinilla, the level of disturbance, while not destructive, is constant with understory clearing and removal of dead wood. Therefore, specialists are likely to struggle to establish themselves and/or to survive. Additionally, the arrival of species is influenced by the surrounding land-use matrix (Chazdon 2003). Since the Sardinilla plantation is surrounded by pastures, generalists have an advantage since they usually have much better dispersal abilities and are often less sensitive to environmental change than specialists (Warren et al. 2001; Krauss, Steffan-Dewenter, and Tscharntke 2003; Larsen, Lopera, and Forsyth 2008). Also, specialists are less likely to be present in high numbers if the conditions in the plantation do not fit their niche or host species preference (Audino, Louzada, and Comita 2014).

Both at the morpho species and functional level, PerMANOVA analysis of the ordination matrix yielded similar relationships, although weaker at the functional level. Treatment (i.e. tree diversity) was significant, but it does not necessarily mean that increasing tree diversity has a positive relationship with beetle diversity. Rather, it means is that treatments (including both the number of tree species and tree species composition) had an influence on beetle assemblages. Therefore, it is important to look at other results of the PerMANOVA, such as the abundance of the different tree species in the plot, to understand what is actually driving the beetle assemblages. In this case, the abundance of two of the focal species *Tabebuia rosea* and *Hura crepitans* as well as the LMA values of Anacardium excelsum were significant. Therefore, I can assume that these tree species are more likely to attract specialists, therefore driving the composition of the beetle community in the plots where they are present (Janzen 1981; Plath, Dorn, Riedel, et al. 2012).

Interestingly, the tree species abundance that was deemed significant when testing the ordination matrix coincides with the dominant tree species in most of the plots (*Tabebuia rosea* and *Hura crepitans*). While this can be a relic of the

higher survival of these species, it can also indicate higher level of specificity being observed on these trees and thus influencing the beetle assemblages. Additionally, the structure of *Anacardium excelsum* and its comparatively large foliar area (Murgas, Barrios, and Luna 2009) can explain the high number of beetles found in its surroundings and the significant influence of its LMA values on the beetle communities at the functional level. Many of the individuals of *Anarcadium excelsum* were also in very good health and filled the physical space of the plantation. Therefore, their foliage would have been easily accessible to establishing species of herbivores.

2.5.3 Environmental variables

Plots were close to each other and it is therefore surprising that beetle assemblages varied across small spatial scales. To be able to act at such a small scale, factors affecting microclimate were deemed important. Canopy openness mostly influences microclimate by the rise in temperature with increasing openness. This is due to more sunlight reaching the understory (Becker, Rabenold, and Idol 1988). There is growing evidence that tropical ectotherms have narrow thermal ranges (Metcalfe et al. 2014). While temperature is not a dramatic limitation factor in the tropics, the correlation between activity and temperature in beetles could explain the importance of this factor in partitioning the communities (Liu, Zhang, and Zhu 1995; Seibold et al. 2016). Any direct temperature regulation could affect herbivore population activity and/or abundance (Bale et al. 2002; Deutsch, Tewksbury, and Huey 2008). The effect of canopy openness may particularly be felt after rain events during the wet season, as sunny areas will dry out more quickly and allow beetles to resume their activities more quickly (Lassau et al. 2005).

Ground vegetation is another component which can regulate microclimate. In the Sardinilla project, the vegetation does not resemble the "natural" state of the forest understory. However, there is a reasonable amount of variation between the plots and the influence of the plant composition on vegetation cover can still be felt. The plant diversity, both functional and taxonomical, is correlated with ecological processes such as decomposition and nutrient cycling and is therefore nonnegligible when investing ecosystem functioning (Symstad 2000; Spasojevic and Suding 2012). However, in the plantation, habitat complexity is controlled to a certain degree, i.e. the plantation is cleaned of its understory once a year, but smaller vegetation is allowed to grow. Nevertheless, it is the tree canopy, shrub canopy, and ground herb cover which form the basis for defining habitat complexity in some studies (August 1983). In the plantation, the present vegetation, apart from the planted trees, is mostly grasses and small shrubs. However, the proportion of grass to shrub changes depending on the dominant tree species in the plot and could therefore favour certain functional groups more than others (Symstad 2000; Petchey and Gaston 2006; Cadotte, Carscadden, and Mirotchnick 2011). Additionally, it has been shown in other contexts that undergrowth can affect herbivore species. Some species will discriminate among trees with and without ground cover. The presence of such ground cover can, in fact, increase abundance and efficiency of predators and parasitoids (Symstad 2000). Therefore, higher vegetation cover can promote suppression of "unnatural" herbivore abundances. Together, canopy openness and vegetation cover influence microclimate within the plantation, even at a small scale, and in turn impact beetle activity and behaviour, ultimately affecting beetle community structure (Lassau et al. 2005). These results suggest that variables influencing microhabitats and their complexity (Lassau et al. 2005) effectively drive beetle assemblages and that smaller scale processes should be taking into consideration.

2.5.4 Stand diversification

In agroecosystems, it is well-established that mixing plant species reduces the abundance of specialized herbivore species when comparing monocultures to poly cultures (Altieri and Nicholls 2004) and these results agree with this pattern. Insect communities can be stabilized in an agro-ecological context in a few different ways. All these techniques have in common that they support natural enemies and inhibit pest attack (Altieri 1999). A key component is that the diversity remains

undisturbed, letting the trophic links that shape and stabilize the insect community strengthen. Mainly, the stability will depend on the density-dependent nature of the trophic levels, where trophic links will respond to changes in the population at other trophic levels (mostly lower levels) (Southwood and Way 1970).

When thinking about multitrophic levels in ecosystems, we have to consider primary production in conjunction with herbivores. If plants exploit resources effectively, it will lead to greater plant productivity (Tilman 1996; Loreau et al. 2001) which would likely increase plant consumption in response (Mulder 1999; Cardinale et al. 2006). However, the direction of this interaction of diversity with primary productivity can be positive or negative (Jactel and Brockerhoff 2007) and it is highly context specific. In the Sardinilla plantation, it has been shown that species composition might be more important in determining productivity than species richness (Salisbury and Potvin 2015). It is also hypothesized that pest problems in forest monocultures is driven more by even-aged structure or intensive silvicultural practices than by the simple species composition of the plantations (Watt 1992). Therefore, species composition, age structure and practices must all be taken into consideration in order to minimize potential pest harms.

While stand diversification has some beneficial effects, the stand composition can have an influence on the strength and direction of the relationship (e.g. Healy, Gotelli, and Potvin 2008; Plath, Dorn, Barrios, et al. 2012; Salisbury and Potvin 2015). The issue in plantations such as Sardinilla, which aim to both promote reforestation and provide a livelihood to the local population, is that tree species have to be a valuable timber species and provide some kind of physical barrier to specialist herbivores. However, if we want to consider herbivores in the management plan, we also have to choose tree species carefully. For example, less phylogenetically similar tree species will be more effective at preventing herbivory in mixed stands (Moreira et al. 2016). However, it is another challenge to find species fulfilling this condition, while also cohabiting well together without excessive competition for resources. More research has to be done in this area to have a definite answer.

2.6 Conclusion

In conclusion, stand diversification had an effect on herbivorous beetles in the Sardinilla plantation. Increasing tree diversity was conducive to functional diversity and evenness, which provide functional redundancy to the ecosystem. This is important for the resilience of the ecosystem, which is key to the sustainability of agroecosystems. Canopy openness and vegetation cover, as well as the identity of some of the focal species, adequately explained drivers of beetle communities in the plantation. Therefore, the results from this study support the idea that management of agroforestry in terms of pests can be done at a local scale. The knowledge from this study supports the use of stand diversification as a means of reducing the harm of herbivory in tropical plantations. All of this evidence also adds support to agroforestry systems as a viable initiative to counter deforestation in Central America.

2.7 Acknowledgments

We would like to thank the many experts at the Canadian National Collection of Insects, Arachnids and Nematodes (Patrice Bouchard, Hume Douglais, Anthony Davies, Anthony Smetana, Serge Laplante, Karine Savard, Yves Bousquet and Robert Anderson) who helped with the identification of the samples. Special thanks to Dr. Hector Barrios at the Universidad de Panama for his ideas and taxonomical help. Special thanks to the members of the Buddle Lab (Chris Cloutier, Shaun Turney, Jessica Turgeon, Gail McInnis and Elyssa Cameron) for their ideas and support and to José Monteza and Lady Mancilla for their help on the field, in Panama. Financial support was provided by NSERC (BESS NSERC-CREATE Grant) and additional funding was provided by the Department of Natural Resource Sciences (McGill) as a Graduate Excellence Award, the National Science and Engineering Council of Canada (NSERC), in the form of a Discovery Grant to Chris Buddle and the Margaret DuPorte Fellowship. I also want to thank the staff at the Smithsonian Tropical Research Institute in Panama for logistical support.

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2.9 Figures and Tables



Figure 2.1 Map of the Sardinilla Plantation, Panama. The black circles showed the randomly chosen plots that were selected for this study. The legend at the bottom left refers to the tree richness in the different plots. Flight-intercept traps were placed at the center of each of the sampled plots.



Figure 2.2 Rank abundance plot for both morpho species (A) and functional groups (B) showing taxa in rank from most to least abundant. Labels show the identification of the 6 most abundant morpho species (A) (Appendix 2.2) and of the 3 most abundant functional groups (B): Phy= Phytophagous (leaf feeders), Pr = Predators and Co = Coprophagous.



Figure 2.3 Rarefaction curves of morpho species richness in A and functional groups in B per tree diversity treatment. 1/Red = 1 tree species, 2/Yellow = 3 tree species, 3/Green = 6 tree species, 4/Blue = 9 tree species and 5/Purple = 18 tree species.



Figure 2.4 Proportion of total individuals of each functional group in each tree diversity treatments. Functional groups are portrayed by the different colours (legend on the right-hand side). The codes refer to groups as follows: Bk = Bark feeders, Co = Coprophagous, Ep = Epiphyte feeders, FI = Flower feeders, Fr = Frugivore, GenHerb = Generalist herbivores, Lt = Litter feeders, Myc = Mycophagous, Nec = Necrophagous, Phy = Phytophagous, Poll = Pollinator and nectar feeders, Pr = Predators, Pr/Nec/Co = Generalist carnivores, Ri = Rizophagous, Sd = Seed-eaters, Wd = Wood borers and Xy = Xylophagous.





Figure 2.5 NMDS ordination of the beetle community across all plots using the log values of morpho species relative abundance in A and functional group abundance in B. Each point indicates the location of a sampled microhabitat the different points and corresponding colour are shown in the legend. Points which are located more closely together are more similar than points located further away from one another. Values for all environmental variables tested are shown in Table 2.1 for A and Table 2.2 for B. The location of each habitat centroid along with the 68% confidence areas is shown.

Table 2.1 PerMANOVA p-values for the effect of treatment, vegetation cover, canopy openness, LMA and abundance of individual tree species on the Bray-Curtis Matrix used for the NMDS Ordination at the morpho species level in Sardinilla, Panama. Here, abundance values are taken from the log total abundance. Significant values are bolded.

Response	Factor	Df	Sum sq	Mean sq	F model	P Value
Bray-Curtis	Treatment	4	1.1468	0.28670	1.4402	0.006 **
Maunx	Vegetation cover	1	0.2876	0.28756	1.4488	0.064.
	Canopy Openness	1	0.4718	0.47182	2.3772	0.001 ***
	LMA Ae	1	0.4227	0.42266	2.10153	0.010 **
	LMA Co	1	0.1731	0.17312	0.86077	0.680
	LMA Hc	1	0.2539	0.25395	1.26264	0.157
	LMA Ls	1	0.2639	0.26389	1.31209	0.114
	LMA Tr	1	0.2015	0.20150	1.00190	0.440
	Abundance Ca	1	0.1948	0.19478	1.0419	0.390
	Abundance Ae	1	0.2496	0.24955	1.3349	0.091.
	Abundance Co	1	0.2345	0.23452	1.2545	0.116
	Abundance Hc	1	0.3192	0.31916	1.7071	0.007 **
	Abundance Ls	1	0.3311	0.33114	1.7713	0.008 **
	Abundance Tr	1	0.3855	0.38547	2.0618	0.001 ***

Table 2.2 PerMANOVA p-values for the effect of treatment, vegetation cover, canopy openness, LMA and abundance of individual tree species on the Bray-Curtis Matrix used for the NMDS Ordination at the functional group level in Sardinilla, Panama. Here, abundance values are taken from the log total abundance. Significant values are bolded.

Response	Factor	Df	Sum sq	Mean sq	F model	P Value
Bray-Curtis Matrix	Treatment	4	0.16236	0.040590	1.5526	0.037 *
	Vegetation cover	1	0.03743	0.037435	1.3830	0.207
	Canopy Openness	1	0.05602	0.056015	2.0695	0.045 *

	LMA Ae	1	0.05729	0.057291	2.05010	0.042 *
	LMA Co	1	0.01937	0.019368	0.69306	0.697
	LMA Hc	1	0.03247	0.032470	1.16191	0.351
	LMA Ls	1	0.02109	0.021091	0.75472	0.667
	LMA Tr	1	0.03126	0.031262	1.11869	0.368
	Abundance Ca	1	0.01238	0.012384	0.48828	0.881
	Abundance Ae	1	0.04247	0.042471	1.67454	0.120
	Abundance Co	1	0.02074	0.020744	0.81788	0.584
	Abundance Hc	1	0.05847	0.058475	2.30552	0.032 *
	Abundance Ls	1	0.03643	0.036432	1.43641	0.200
	Abundance Tr	1	0.05507	0.055073	2.17141	0.028 *

Table 2.3 ANOVA *p*-values for the effect of treatment and dominant tree species on the total abundance, richness, and diversity of beetles in Sardinilla, Panama, at the functional level. Here, abundance values are taken from the log total abundance. Significant values are bolded.

Response	Factor	Df	Sum sq	Mean sq	F model	P Value
Abundance	Treatment	4	0.24166	0.060416	0.3677	0.8254
	Dom Tree Spp	4	1.00775	0.251937	1.5332	0.2809
	Treatment:DomTree Spp	4	0.29482	0.073705	0.4485	0.7713
Species	Treatment	4	5.2381	1.3095	0.4042	0.8009
Richness	Dom Tree Spp	4	13.0338	3.2584	1.0058	0.4584
	Treatment:DomTree Spp	4	5.0495	1.2624	0.3897	0.8107
Simpson's Index	Treatment	4	0.005959	0.0014898	0.3655	0.82683
	Dom Tree Spp	4	0.060435	0.0151087	3.7068	0.0543
	Treatment:DomTree Spp	4	0.028321	0.0070802	1.7371	0.23456

Fisher's alpha	Treatment	4	0.81274	0.20319	0.5726	0.6905
	Dom Tree Spp	4	0.19300	0.04825	0.1360	0.9644
	Treatment:DomTree Spp	4	0.83726	0.20931	0.5899	0.6796
Pielou's evenness	Treatment	4	0.0003183	0.0000796	0.1638	0.950911
	Dom Tree Spp	4	0.0174093	0.0043523	8.9578	0.004739
	Treatment:DomTree Spp	4	0.0026070	0.0006517	1.3414	0.334463

2.10 Appendix

Family	Reference	Taxa (if specific)	Taxonomic level
Multiple families	(Arguedas, Chaverri, and Verjans 2004)		
	(Arnett, Downie, and Jaques 1980)		
	(Arnett et al. 2002)		
	(Barrios 2003)		
	(Boulanger, Sirois, and Hébert 2010)		
	(Cabrera, Robaina, and León 2011)		
	(Corrêa, Almeida, and Moura 2014)		
	(Delgado and Couturier 2014)		
	(Garay 2012)		
	(Goeden 1971)		
	(González-Vainer and Morelli 2008)		
	(Janzen 1976)		
	(Jirón and Cartín 1981)		
	(Kartohardjono 1988)		
	(Klepzig et al. 2012)		
	(Marinoni et al. 2001)		
	(Moser 2006)		
	(Ødegaard 2004)		
	(Päivinen et al. 2003)		
	(Paredes and Tello 2016)		
	(Peck, Thomas, and Jr 2014)		
	(Santos, Almeida, and Araújo 2009)		
	(Silberbauer-Gottsberger 1973)		
	(Thien, White, and Yatsu 1983)		
	(Tomanova, Tedesco, and Campero 2007)		
	(Ulyshen and Hanula 2010)		
	(Winder and Harley 1983)		
	(Zelada et al. 2015)		
	(Zilli, Montalto, and Marchese 2008)		
Anobiidae	(White 1975)		

Appendix 2.1 List of references used to determine functional groups for all morpho species and corresponding bibliography

Carabidae	(Arndt and Kirmse 2002)	Harpalini	Tribe
	(Mitchell 1963)	Bembidion	Genus
	(Nyundo and Yarro 2007)		
	(Topoff 1969)	Helluomorphoides	Genus
	(Weber, Rowley, and Greenstone 2006)	Lebia	Genus
Cerambycidae	(Di Lorio 1997)		
	(Gosling 1984)		
	(Martínez 2000)		
	(Micheli 2006)		
	(Swift et al. 2010)		
	(Toledo, Corona, and Morrone 2007)		
Cerylonidae	(Dajoz 1992)		
Chelonariidae	(Mequignon 1934)	Chelonarium	Genus
Chrysomelidae	(Barney, Clark, and Riley 2009)	Alticini	Tribe
	(Begossi and Benson 1988)	Alticinae	Subfamily
	(Cabrera and Durante 2001)	Acalymma	Genus
	(Chamorro 2013)	Cryptochephalini	Tribe
	(Clark 2004)		
	(Franz 2009)	Eustylini	Tribe
	(Jolivet 1987)	Megascelinae Eumolpinae	Subfamily
	(Jolivet 1991)	Alticinae	Subfamily
	(Jolivet and Hawkeswood 1995)		
	(Krysan and Smith 1987)	Diabrotica	Genus
	(Mann and Crowson 1981)	Syneta	Genus
	(Reyes, Canto, and Rodríguez 2009)	Megacerus	Genus
	(Romero and Ayers 2002)	Amblycerus	
	(Parry 1974)	Dibolia	Genus
	(Richards and Coley 2008)		
	(Romero and Johnson 2000)	Zabrotes	Genus
	(Strother and Staines 2008)	Fidia	Genus
	(Vecco et al. 2009)	Syphrea	Genus
Coccinellidae	(Almeida, Corrêa, and Giorgi 2011)		
	(Cranshaw 2001)		
	(Gordon 1985)		
	(Yoshida and Mau 1985)	Nephaspis	Genus
Curculionidae	(Atkinson and Equihua 1986)	Scolytinae	Subfamily

	(Barrios-Izas, Anderson, and Morrone 2016)	Conotrachelini	Tribe				
	(Fassbender, Baxt, and Berkov 2014)						
	(Greco and Wright 2015)	Xylosandrus	Genus				
	(Halmschlager, Ladner, and Zabransky 2007)	Pentarthrum	Genus				
	(Hernandez 2010)						
	(Heard and Forno 1996)	Coelocephalapion	Genus				
	(Janzen 1982)	Cleogonus	Genus				
	(Korotyaev 2008)	Ceutorhynchinae	Subfamily				
	(O'Brien and Wibmer 1982)						
	(Pinzón-Navarro, Barrios, and Múrria 2010)	Conotrachelus	Genus				
	(Reichert, Johnson, and Chacón 2010)	Cryptorhynchus	Genus				
	(Rheinheimer 2006)	Ithaura	Genus				
	(Río, Morrone, and Lanteri 2015)	Naupactini	Tribe				
	(Santos et al. 2015)	Rhyssomatus	Genus				
Dysticidae	(Alarie and Michat 2014)						
	(Megna and Epler 2012)	Copelatus	Genus				
	(Velasco and Millan 1998)	Thermonectus	Genus				
Elateridae	(Douglas 2006)	Cardiophorinae	Subfamily				
	(Johnson 2015)	Drapetes	Genus				
	(Johnson 2017)	Dipropus	Genus				
	(Martínez-Luque and Zurita-García 2016)						
Endomychidae	(Tomaszewska 2000)						
	(Yoder, Denlinger, and Wolda 1992)	Stenotarsus	Genus				
Erotylidae	(McHugh and Chaboo 2015)						
	(Medrano-Cabral, Bastardo, and Skelley 2009)	Aegithus	Genus				
	(Moreira, Moreira, and Andaló 2010)	Mycotretus	Genus				
	(Skelley 1999)						
Hydraenidae	(Collantes and Soler)	Hydraena	Genus				
Hydrophilidae	(Fikáček 2009)	Cercyon	Genus				
	(Fikáček and Trávníček 2009)	Georissinae	Subfamily				
Lampyridae	(Viviani 2001)						
Lycidae	(Bocak and Bocakova 2008)						
Monotomidae	(Bousquet 2003)	Europs	Genus				
Nitidulidae	(Cline 2003)	Camptodes	Genus				
	(Cline and Kinnee 2012)	Lobiopa	Genus				
	(Weiss and Williams 1980)	Stelidota	Genus				

Ptilodactylidae	(Stribling and Seymour 1988)						
Scarabeidae	(Deloya 1992)						
	(Edmonds and Zídek 2010)	Coprophanaeus	Genus				
	(Halffter, Favila, and Halffter 1992)						
	(Horgan 2002)						
	(Howden, Howden, and Holloway 2007)	Balboceratini	Tribe				
	(King 1984)	Phyllophaga	Genus				
	(Nichols et al. 2008)	Scarabeinae	Subfamily				
	(Pardo-Locarno 2015)	Melolonthinae	Subfamily				
Scirtidae	(Ruta, Klausnitzer, and Prokin 2017)						
Staphylinidae	(Cameron 1922)						
	(Chani-Posse 2004)	Philonthus	Genus				
	(Eghtedar 1970)	Philonthus	Genus				
	(Ogawa and Löbl 2016)	Xotidium	Genus				
	(Schmidt 1999)	Paederinae Staphylininae					
Tenebrionidae	(Bouchard, Lawrence, and Davies 2005)						
	(Cabrera-Asencio and Santiago-Blay 2003)	Epitragus	Genus				
	(Ferrer and Delatour 2007)	Goniadera	Genus				
	(Jiménez-Sánchez and Juárez-Gaytán 2015)						
	(Luna 2004)						
	(Watt 1974)						

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ID	Family	Subfamily	Genus	Species Name	FunctionalGroup	Reference
1	Scarabeidae	Melolonthinae	Phyllophaga	1	Filorizofage	(King, 1984)
2	Scarabeidae	Aphodiinae	Ataenius	1	Coprophage	(Arnett et al., 2002)
3	Scarabeidae	Bolboceratinae	Neoathyreus	1	Fungi/Plant leaves	(Howden et al., 2007)
4	Trogidae		Trox	1	Coprophage	(Deloya et al., 1992)
5	Scarabeidae	Scarabeinae	Coprophanaeus	1	Coprophage	(Edmonds et al., 2010)
6	Scarabeidae	Scarabeinae	Coprophanaeus	2	Coprophage	(Edmonds et al., 2010)
7	Scarabeidae	Cetoniinae	Marmarina	maculos a	Frugivore	(Pardo-Locarno, 2015)
8	Scarabeidae	Scarabeinae	Canthon	cyanellu s	Necrophage	(Halffter et al., 1992)
9	Scarabeidae	Scarabeinae	Canthon	1	Predator/Necrophage/Coprophage	(Nichols et al., 2008)
10	Scarabeidae	Scarabeinae	Canthon	2	Predator/Necrophage/Coprophage	(Nichols et al., 2008)
11	Scarabeidae				Coprophage	(Deloya et al., 1992)
12	Scarabeidae	Aphodiinae	Aphodius	1	Coprophage (Herbivore)	(Horgan, 2002)
13	Scarabeidae	Scarabeinae	Canthon	3	Predator/Necrophage/Coprophage	(Nichols et al., 2008)
14	Scarabeidae	Scarabeinae	Canthon	4	Predator/Necrophage/Coprophage	(Nichols et al., 2008)
15	Scarabeidae	Scarabeinae	Canthon	5	Predator/Necrophage/Coprophage	(Nichols et al., 2008)
16	Elateridae	Elaterinae	Dipropus	1	Flowers and/or phytophilous and floricolous arthropods	(Johnson, 2017)
17	Elateridae	Elaterinae	Diplostethus	1	Filophagus	(Martínez-Luque, 2016)

Appendix 2.2 List of all morpho species with information on taxonomy and functional diversity. References used are listed in Appendix 2.1

18	Elateridae	Elaterinae	Dipropus	2	Flowers and/or phytophilous and floricolous arthropods	(Johnson, 2017)	
19	Elateridae	Cardiophorinae	Esthesopus	1	Also pollinators	(Douglas, 2006)	
20	Elateridae	Elaterinae	Physorhinus	1	Phytophagous	(Winder and Harley, 1983)	
21	Elateridae	Elaterinae	Anoplischius	1	Phytophagous	(Winder and Harley, 1983)	
22	Elateridae	Elaterinae	Anoplischiopsis	1	Phytophagous + roots (larvae)	(Cabrera et al., 2011)	
23	Elateridae	Elaterinae	Anoplischiopsis	2	Phytophagous + roots (larvae)	(Cabrera et al., 2011)	
24	Elateridae	Elaterinae	Anoplischiopsis	3	Phytophagous + roots (larvae)	(Cabrera et al., 2011)	
25	Dytiscidae	Hydroporinae	Desmopachria	1	Other arthropods	(Alarie and Michat, 2014)	
26	Dytiscidae	Copelatinae	Copelatus	1	Other arthropods	(Megna and Epler, 2012)	
27	Dytiscidae	Dysticinae	Thermonectus	1	Other arthropods	(Velasco and Millan, 1998)	
28	Dytiscidae	Copelatinae	Copelatus	2	Other arthropods	(Megna and Epler, 2012)	
29	Noteridae						
30	Hydrophilidae	Hydrophilinae	Enochrus	1	Collector gatherers	(Zilli et al., 2008)	
31	Hydrophilidae	Hydrophilinae	Enochrus	2	Collector gatherers	(Zilli et al., 2008)	
32	Hydrophilidae						
33	Hydrophilidae	Sphaeridiinae	Cercyon	1	Coprophage (Herbivore)	(Fikacek, 2009)	
34	Hydrophilidae						
35	Dermestidae						
36	Dermestidae						
37	Dermestidae						
38	Dermestidae						
39	Dermestidae						
40	Staphylinidae	Scydmaeninae	Euconnus	1	Ant associated	(Päivinen et al., 2003)	
41	Anobiidae						
42	Anobiidae						
43	Anobiidae						
44	Anobiidae						
45	Anobiidae						
46	Anobiidae						
47	Curculionidae	Entiminae	Eustylus	sexgutt atus	Roots (larvae) and leaves (adults)	(Franz, 2009)	
48	Curculionidae	Curculioninae	Myrmex	1	Phylophagous (new leaves)	(Barrios, 2003)	
49	Curculionidae	Conoderinae	Macrocopturus	lamprot horax	Buds and shoots	(Delgado and Couturier,2014)	
50	Chrysomelidae	Eumolpinae	Fidia	1	Leaves and buds	(Strother and Staines, 2008)	
51	Coccinellidae	Sticholotidinae	Cephaloscymnus	1	Other insects	(Almerida et al., 2011)	
52	Curculionidae	Apioninae	Coelocephalapion	1	Leaves and flower buds	(Heard and Forno, 1996)	
53	Curculionidae	Molytinae	Cleogonus	1	Seed predation	(Janzen, 1982)	

54	Curculionidae	Molytinae	Heilipodus	1	Young leaves and buds	(O'Brien and Wibmer, 1982)
55	Curculionidae	Molytinae	Zascelis	1	Bark	(Gomez Hernandez, 2010)
57	Curculionidae	Conoderinae	Zygops	1	Saproxylic	(Fassbender et al., 2014)
58	Curculionidae	Molytinae	Cryptorhynchus	1	Stem boring	(Reichert et al., 2010)
59	Curculionidae	Molytinae	Rhyssomatus	1	Seed feeding	(Santos et al., 2001)
60	Curculionidae	Entiminae	Anypotactus	jansoni	Phytophagous	(Río et al., 2015)
61	Curculionidae	Baridinae	Glyptobaris	1	Flower and pollination	(Thien et al., 1983)
62	Curculionidae	Molytinae	Rhyssomatus	2	Seed feeding	(Santos et al., 2001)
64	Chelonariidae		Chelonarium	1	Epiphyte	(Mequignon, 1934)
65	Curculionidae	Molytinae	Zascelis	2	Bark	(Gomez Hernandez, 2010)
66	Curculionidae		Eutinobithrus	1	Phytophagous	(Tomanova et al., 2007)
67	Curculionidae					
68	Curculionidae	Molytinae	Zascelis	3	Bark	(Gomez Hernandez, 2010)
69	Curculionidae	Ceutorhynchina e	Hypocoeloides	1	Onagracea and Vitaceae	(Korotyaev, 2008)
70	Curculionidae	Molytinae	Fiedlerius	1	Dead leaves	(Reichert et al., 2010)
71	Curculionidae	Molytinae	Aeatus	1	Dead leaves	(Barrios-Izas and al., 2016)
72	Curculionidae	Molytinae	Cryptorhynchus	2	Stem boring	(Reichert et al., 2010)
73	Chrysomelidae	Galerucinae	Distigmoptera	1	Phylophagous	(Jolivet, 1991)
74	Curculionidae	Baridinae				
76	Chrysomelidae	Bruchinae	Kytorhinus?	1		
77	Curculionidae					
78	Curculionidae					
79	Hydrophilidae	Georissinae	Georissus	1	Decaying organic particles in mud	(Fikáček and Trávníček, 2009)
80	Curculionidae	Scolytinae	Xyleborus	1	Saproxylic	(Lanuza Garay and Vargas Cusatti, 2012)
81	Chrysomelidae	Bruchinae			Seed eating	(Romero et al., 2002)
82	Cerylonidae		Cerylon		Saproxylic	(Dajoz, 1992)
83	Curculionidae	Scolytinae			Xylophagous	(Atkinson and Equihua, 1986)
84	Aderidae		Zonantes		Saproxylic	(Klepzig et al., 2012)
85	Chrysomelidae	Eumolpinae	Rhapdopterus	1	Defoliating (leaves)	(Arguedas et al., 2004)
86	Chrysomelidae	Cryptocephalina e	Cryptocephalus	1	Leaves and flowers	(Chamorro, 2013)
87	Chrysomelidae	Cryptocephalina e	Cryptoceph	1	Phytophagous	(Chamorro, 2013)
88	Chrysomelidae	Cryptocephalina e	Cryptocephalus	2	Leaves and flowers	(Chamorro, 2013)
89	Chrysomelidae	Galerucinae	Diabrotica	1	Phylophagous	(Krysan and Smith, 1987)
90	Chrysomelidae	Galerucinae	Omophoita	1	Phylophagous	(Begossi and Benson, 1988)

91	Carabidae	Harpalinae	Lebia	1	Other insects (beetles)	(Weber et al., 2006)
92	Chrysomelidae	Galerucinae	Capraita	1	Phylophagous	(Jolivet, 1991)
93	Chrysomelidae	Galerucinae	Distigmoptera	2	Phylophagous	(Jolivet, 1991)
94	Chrysomelidae	Galerucinae	Diabrotica	2	Phylophagous	(Krysan and Smith, 1987)
95	Chrysomelidae	Galerucinae	Capraita	2	Phylophagous	(Jolivet, 1991)
96	Chrysomelidae	Galerucinae	Kuschelina	1	Phylophagous	(Barney et al., 2009)
97	Chrysomelidae	Galerucinae	Dibolia	1	Phylophagous and leaf miners	(Parry, 1974)
98	Chrysomelidae	Eumolpinae	Colapsis	1	Phylophagous	(Zelada et al., 2015)
99	Chrysomelidae	Eumolpinae	Syneta	1	Phylophagous	(Mann and Crowson, 1981)
100	Chrysomelidae	Galerucinae	Kuschelina	2	Phylophagous	(Barney et al., 2009)
101	Chrysomelidae	Galerucinae	Omophoita	2	Phylophagous	(Begossi and Benson, 1988)
102	Chrysomelidae	Galerucinae	Acalymma	1	Pollen feeding	(Cabrera and Durante, 2001)
103	Chrysomelidae	Cryptocephalina e	Cryptocephalus	3	Leaves and flowers	(Chamorro, 2013)
104	Chrysomelidae					
105	Chrysomelidae	Galerucinae	Glyptina	1	Feed on Euphorbiaceae	(Clark et al. 2004)
106	Chrysomelidae	Galerucinae	Systena	1	Phylophagous	(Jolivet and
107	Ptilodactylidae	Dryopoidea	Ptilodactyla		Myco/phylophagous	Hawkeswood, 1995) (Stribling and Seymour, 1988)
108	Endomychidae	Stenotarsinae	Stenotarsus	1	Mycophagous	(Yoder et al., 1992)
109	Scirtidae					(Santos et al., 2009)
110	Chrysomelidae					
111	Coccinellidae	Scymninae			Other arthropods	(Gordon, 1985)
113	Chrysomelidae	Eumolpinae			Phylophagous	(Jolivet, 1987)
114	Coccinellidae	Scymninae	Nephaspis	1	Other arthropods	(Yoshida and Mau, 1985)
115	Chrysomelidae	Galerucinae			Phylophagous	(Marinoni et al., 2001)
116	Scirtidae		Scirtes	1	Flowers	(Ruta et al., 2017)
117	Latridiidae					
118	Coccinellidae	Scymninae	Didion	1	Carnivorous (spider mites)	(Gordon, 1985)
119	Chrysomelidae	Galerucinae	Unknow/Damage d			(Marinoni et al., 2001)
120	Monotomidae	Monotominae	Europs	1	Roots	(Bousquet, 2003)
121	Chrysomelidae					
122	Chrysomelidae	Eumolpinae	Colapsis	2	Phylophagous	(Zelada et al., 2015)
123	Chrysomelidae	Eumolpinae	Colapsis	3	Phylophagous	(Zelada et al., 2015)
124	Chrysomelidae					
125	Scirtidae					(Santos et al., 2009)
126	Chrysomelidae	Cassidinae				
127	Chrysomelidae	Eumolpinae	Megascelis	1	Phylophagous	(Jolivet, 1987)
128	Chrysomelidae					

129	Chrysomelidae	Chrysomelinae	Phratora	1	Phylophagous	(Richards and Coley, 2008)
130	Chrysomelidae	Chrysomelinae	Phratora	2	Phylophagous	(Richards and Coley, 2008)
131	Chrysomelidae	Eumolpinae	Rhapdopterus	2	Defoliating (leaves)	(Arguedas et al., 2004)
132	Chrysomelidae	Eumolpinae	Colapsis	4	Phylophagous	(Zelada et al., 2015)
133	Chrysomelidae	Galerucinae	Syphrea	1	Phylophagous (new and young leaves) + possibly pollen	(Vecco et al., 2009)
134	Chrysomelidae	Bruchinae	Zabrotes	1	Seed eating (Fabaceae)	(Romero and Johnson, 2000)
135	Chrysomelidae	Bruchinae	Amblycerus	1	Seed eating	(Romero et al., 2002)
136	Chrysomelidae	Eumolpinae	Colapsis	5	Phylophagous	(Zelada et al., 2015)
137	Lycidae			1	Nectar	
138	Cerambycidae	Dorcasta	dasycera		Phytophagous	(Goeden, 1971)
139	Lycidae			4	Nectar	(Bocak and Bocakova, 2008)
140	Lycidae			2	Nectar	(Bocak and Bocakova, 2008)
141	Lycidae	Lycinae	Calopteron	1	Nectar	(Bocak and Bocakova, 2008)
142	Lycidae			3	Nectar	(Bocak and Bocakova, 2008)
143	Lampyridae	Lampyrinae	Lamprocera	picta	Small insects and gastropods	(Viviani, 2001)
144	Cerambycidae	Cerambycinae	Stizocera	rugicolli s	Phytophagous	(Martínez, 2000)
145	Cerambycidae	Lamiinae	Hyperplatys	1	Bark and leaves	(Gosling, 1984)
146	Cerambycidae	Adetus	bacillarius	1	Wood borers	(Ødegaard, 2004)
147	Cerambycidae	Lamiinae	Laticranium	mandib ulare	Phylophagous	(Di Iorio, 1997)
148	Cerambycidae			1	Wood borers	(Swift et al., 2010)
149	Tenebrionidae	Lagriinae	Statira	1	Phylophagous (coffee trees)	(Peck et al., 2014)
150	Carabidae	Harpalinae	Helluomorphoides	1	Feeding on ants	(Topoff, 1969)
151	Carabidae	Harpalinae	Lebia	2	Other insects (beetles)	(Weber et al., 2006)
152	Carabidae	Harpalinae	Pentagonica	1		(Nyundo and Yarro, 2007)
154	Carabidae	Trechinae	Bembidion	1	Prey or remains	(Mitchell, 1963)
155	Carabidae	Harpalinae			Can feed on seeds	(Arndt and Kirmse, 2002)
156	Cerambycidae	Lamiinae	Lepturges		Wood borers	(Gosling, 1984)
157	Cerambycidae	Neocompsa	alacris		Wood borers	(Toledo et al., 2007)
158	Cucujidae					
159	Cucujidae					
160	Cleridae	Clerinae	Priocera	1	Bark	(Ulyshen and Hanula, 2010)
161	Tenebrionidae	Lagriinae	Goniadera	1	Rotten wood	(Ferre and Delatour, 2007)
162	Tenebrionidae	Tenebrioninae	Penichrus	1	Living and dead leaves	(Bouchar et al., 2005)
163	Tenebrionidae	Alleculinae	Lobopoda	aeneoti ncta	Dead leaves	(Moser, 2006)

164	Tenebrionidae	Alleculinae	Cteisa	pedinoi des	Dead leaves	(Watt, 1974)
165	Tenebrionidae	Alleculinae	Xystropus	californi cus	Flowers	(Silberbauer- Gottsberger, 1973)
166	Tenebrionidae	Alleculinae	Lobopoda	punctico Ilis	Dead leaves	(Moser, 2006)
167	Tenebrionidae	Alleculinae	Xystropus	lebasii	Flowers	(Silberbauer- Gottsberger, 1973)
168	Elateridae	Lassoninae	Drapetes	plagiatu s	Other insects	(Johnson, 2015)
169	Buprestidae				Phytophagous, wood borers, dead trees,	http://delta- intkey.com/elateria/w ww/bupr.htm
170	Curculionidae	Molytinae	Ithaura	1	Leaves and fruits	(Rheinheimer, 2006)
171	Curculionidae	Cossoninae	Pentarthrum	1	Wood borers	(Halmschlager et al., 2007)
172	Ciidae					
173	Chrysomelidae	Bruchinae	Pachymerus	1	Seed eating	(Janzen, 1976)
174	Chrysomelidae	Bruchinae	Amblycerus	2	Seed eating	(Romero et al., 2002)
175	Chrysomelidae	Bruchinae	Megacerus	1	Seed eating	(Reyes et al., 2009)
176	Anobiidae				Wood boring	(White, 1975)
177	Curculionidae	Scolytinae	Xylosandrus	1	Xylophagous	(Greco and Wright, 2015)
178	Brenthidae	Brenthinae	Brenthus	1	Leaves and fruits	(Parades and Tello, 2016)
179	Mordellidae		Mordella	1	Flowers	(Goeden, 1971)
180	Staphylinidae	Schapidiinae	Toxidium	1	Other arthropods	(Ogawa and Löbl, 2016)
181	Carabidae	Trechinae	Bembidion	2	Prey or remains	(Mitchell, 1963)
182	Carabidae	Harpalinae	Galerita	1	Other insects (Caterpillar)	(Arnett et al., 1980)
183	Carabidae	Harpalinae				(Weber et al., 2006)
184	Carabidae					
185	Carabidae					
186	Carabidae					
187	Anthicidae					
188	Limnebiidae					
189	Nitidulidae					
190	Nitidulidae					
192	Hydraenidae	Hydraeninae	Hydraena	1		(Collantes and Soler, 1996)
193	Histeridae					
194	Coccinelidae	Sticholotidinae	Coccidophilus	1	Scale insects (+ supplement on pollen and nectar)	(Cranshaw, 2001)
195	Cerocanthidae				·	
196	Staphylinidae	Staphylininae	Philonthus	1	Dung-eating flies	(Chani-Posse, 2004)
197	Staphylinidae	Xantholiniae		1	Other arthropods	(Cameron, 1922)
198	Staphylinidae	Paederinae	Paederus	1		(Kartohardjono, 1988)
199	Staphylinidae	Dermaptera	1			

200	Staphylinidae	Staphylininae	Oligotergus	1	Necrophagous	(Jiménez-Sánchez, 2011)
201	Staphylinidae	Xantholiniae		2	Other arthropods	(Cameron, 1922)
202	Staphylinidae	Staphylininae	Atanygnathus	1	Necrophagous	(Márquez Luna, 2004)
203	Staphylinidae	Paederinae	Palaminus	1		(González-Vainer and Morelli, 2008)
204	Staphylinidae	Paederinae	Medon	1	Fly larvae	(Schmidt, 1999)
205	Staphylinidae	Oxytelinae	Anotylus	1	Larvae and eggs	(Eghtedar, 1970)
206	Staphylinidae	Tachyporinae	Coproporus	1	Coprophage and necrophage	(Corrêa, et al., 2014)
207	Staphylinidae	Pselaphinae	Cteninis	1	Mites and collembola	(Arnett and Thomas, 2000)
208	Erotylidae	Megalodactnina e	Megalodacne	fasciata	Plants and fungus	(Skelley, 2008)
209	Erotylidae		Aegithus	1	Plants and fungus	(Medrano-Cabral et al., 2009)
210	Erotylidae		Mycotretus	1	Fungi	(Moreira et al., 2010)
211	Nitidulidae	Nitidulinae	Lobiopa	1	Sap feeding, frugivore	(Cline and Kinnee, 2012)
212	Erotylidae		Mycophtorus	1	Fungi	(McHugh and Chaboo, 2015)
213	Erotylidae	Nitidulinae	Stelidota	1	Sap feeding, frugivore	(Weiss and Williams, 1980)
214	Erotylidae	Nitidulinae	Camptodes	1	Flowers and vegetation	(Cline, 2003)
215	Nitidulidae					
216	Erotylidae		Mycotretus	2	Fungi	(Moreira et al., 2010)
217	Endomychidae					
218	Dytiscidae	Copelatinae	Copelatus	1	Aquatic insects	(Megna and Epler, 2012)
219	Erotylidae		Mycotretus	sexpunc tatus	Fungi	(Moreira et al., 2010)
220	Endomychidae	Anidrytus			Fungi	(Tomaszewska, 2000)
221	Erotylidae		Mycotretus	3	Fungi	(Moreira et al., 2010)
222	Erotylidae	Nitidulinae	Camptodes	2	Flowers and vegetation	(Cline, 2003)
223	Coccinellidae	Sticholotidinae	Cephaloscymnus	2	Other insects	(Almerida et al., 2011)
224	Nitidulidae					
225	Erotylidae					
226	Erotylidae	Nitidulinae	Stelidota	2	Sap feeding, frugivore	(Weiss and Williams, 1980)
227	Erotylidae	Nitidulinae	Stelidota	3	Sap feeding, frugivore	(Weiss and Williams, 1980)
228	Elateridae					
229	ABC					
230	AB01					
231	AB02					
232	AB03					
233	Dermestidae				Mammal corpse	(Jirón and Cartín, 1981)
234	Unknown					
235	Cerambycidae	Leptostylopsis			Wood borers	(Micheli, 2006)

236	Curculionidae	Molytinae	Conotrachelus	1	Seed eating		(Pinzć
							al., 20
238	Curculionidae						
239	Chrysomelidae	Galerucinae				(Marinoni et al., 2001)	
240	Corylophidae	Corylophinae	Clypastraea	1	Mycophagous	(Boulanger et al., 2010)	
241	Elateriformia						
242	Tenebrionidae	Pimeliinae	Epitragus	1	Leaves and fruits	(Cabrera-Asencio et al., 2003)	

Connecting statement

The overarching theme of this thesis is to explore the relationships between stand diversification and beetle herbivores. Chapter 2 provided information on the effect on stand diversification on beetle communities as a tool to lessen herbivory damage and also highlighted key environmental variables at play.

While Chapter 2 took a more traditional descriptive approach, the following chapter will use Structural Equation Modeling to help us gain a better understanding of the relationship between herbivory and ecosystem functioning in the system. In particular, chapter 3 explores the loop between beetle communities, herbivory and aboveground biomass, with links with canopy openness and carbon uptake. Since this chapter is exploratory, it also provides recommendations for future investigation of the relationship in the plantation.

Chapter 3: Structural Equation Modeling of beetle herbivores and ecosystem functioning in Sardinilla, Panama

3.1 Abstract

Using pastures for afforestation is considered an effective measure to sequester carbon and help reverse the effects of deforestation. While mature tropical forests are preferred, those ecosystem services could also be obtained from naturally regenerating forests or plantations. Yet, herbivore damage has been shown to influence ecosystem processes. Structural equation modeling (SEM) is a multivariate statistical method with which we can evaluate a network of relationships between manifest and latent variables. This chapter uses SEM to create a model of herbivory between beetle communities, herbivory and above ground biomass, with links to canopy openness and carbon uptake in the Sardinilla plantation. The variables leaf-mass area (LMA), leaf nitrogen content (LNC) and specific leaf area (SLA) were indicators of the latent variable "Herbivory" and functional diversity and beetle abundance were indicators of "Beetle diversity". The other variables present in the model are canopy openness, aboveground biomass and carbon uptake. After testing my theoretical model against several other versions within the conceptual framework, I settled on the original model. While even this model did not provide a very good fit to the data, it was still considered the best model using several estimation parameters. The major finding of this exploratory analysis is that a negative relationship exists between aboveground biomass and beetle diversity and between beetle diversity and herbivory. Additionally, biomass seemed to be the most important determinant of herbivory, as defined in our study. Some of the recommendations from this study are to increase sampling effort, temporally and spatially, as well as diversifying sampling traps. Also, performing analysis at the individual tree level as well as at the plot level would be preferred. In order to gain a more complete picture of the beetle diversity, it would be important to capture the leaf phenology and add this parameter to the analysis. Finally, using more context-specific ecosystem functioning measurements instead of more general measurements will improve the fit of the model.

3.2 Introduction

High rates of deforestation have been observed in the tropics. The situation in Panama and in neighbouring countries has been deteriorating dramatically over the last few decades. Conversion of land to pasture resulted in extensive grazing and changes in ecosystem functioning, especially in increasing CO₂ concentrations in the atmosphere (Wassenaar et al. 2007). While different types of land can be used for afforestation, using pastures in that matter is considered an effective measure to sequester carbon. Such measures could mitigate the increasing CO₂ concentrations (FAO 2009) and reverse the effects of deforestation. Malhi, Meir, and Brown (2002) estimated that such efforts in tropical regions could provide a mitigation potential of 15% of global CO₂ emissions. But, while the importance of tropical forests in carbon sequestering is well documented, deforestation continues (FAO 2006). Although mature tropical forests are preferred for their ecosystem services (Hall et al. 2011), it has been suggested that some of those services could be obtained from naturally regenerating forests or plantations (Lamb, Erskine, and Parrotta 2005; Oliver and Mesznik 2006; Chazdon 2008; Benavas et al. 2009). Yet, herbivore damage has been shown to influence ecosystem processes such as transpiration, tree growth, tree mortality and light penetration to the forest floor (Stephens, Turner, and Roo 1972; Campbell and Sloan 1977; Houston, Parker, and Wargo 1981; Lovett et al. 2002).

While an experimental approach is necessary to demonstrate mechanisms underlying ecological processes, observational and exploratory analysis can complement and guide future studies in an experimental context. In ecology, we are interested in processes comprised of a multitude of variables. Therefore, partitioning the processes into sub-processes and causal interactions is useful to translate the mechanisms in a way where they can be studied. Understanding selected measurements can help us understand the mechanism as a whole.

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Structural equation modeling (SEM) is a multivariate statistical method with which we can evaluate a network of relationships between manifest (from here on called indicators) and latent variables (Arhonditsis et al. 2006). By using SEM, we can get an idea of the mechanisms in place and test hypotheses about them (Agrawal et al. 2007). The advantage of using SEM is that all coefficients in the model are estimated simultaneously (Dion 2008). This method allows us to assess the significance and strength of beetle herbivores in the context of the whole plantation model.

Several studies that have explored the relationships of herbivory with a number of leaf functional traits have arrived at different conclusions regarding the relative importance of these traits for insect herbivores (Cárdenas et al. 2014; Schuldt et al. 2014) and no general pattern has emerged. A higher herbivory was reported on woody plants with a larger species-specific leaf size (Cárdenas et al. 2014; Zava and Cianciaruso 2014), while the association between herbivory and leaf thickness (toughness or specific leaf weight) can vary from negative (Coley 1983; Alliende 1989) to nonsignificant (Cárdenas et al. 2014) or even positive (Poorter, Plassche, and Willems 2004). These discrepancies suggest that prediction of plant losses to herbivores must consider other dimensions of plant ecological strategies simultaneously with leaf functional traits. Furthermore, the associations between foliar losses to insects and plant functional traits may vary among localities due to variations in climate, soil fertility and the availability of other resources (Wise and Abrahamson 2007).

The primary objective of this research is to use SEM to create a model of herbivory by beetles in the Sardinilla plantation. The secondary goal is to use these results to provide recommendations for future projects investigating the role of insect herbivores in tropical agroforestry and reforestation initiatives.

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3.3 Methods

3.3.1 Study site

The study was conducted in the Sardinilla plantation located in Sardinilla in the Buena Vista region of central Panama (9°19'30" N, 79°38'00 "W), approximately 20 km from Barro Colorado Island (BCI) (Scherer-Lorenzen, Bonilla, and Potvin 2007a). The plantation is dedicated to understanding the complex links between ecosystem biogeochemical cycling, especially carbon cycling, land use, and biodiversity in tropical environments over the long term. This experiment site is designed in a way to explore structural diversity of successional communities in a semi-natural way for the region and, especially, to develop sustainable agroecosystems in the Neotropics. The plantation relies on native tree species from Central Panama and replicates the species composition from the nearby island of Barro Colorado. In 2001, the experimental plantation was established, with the use of six native tree species. Twenty-four diversity plots were planted: six 6-species and six 3-species plots as well as 12 monocultures) (Scherer-Lorenzen, Bonilla, and Potvin 2007), where the treatments were randomly assigned. For this study, I selected 5 monoculture plots, one for each focal species except for Cordia alliodora since most specimens died during the first season, 5 of the three-species plot and 5 of the six-species plot, at random. Additionally, a second plantation was established in 2002 with treatments of six, nine or 18 species. For this plantation, I selected two of each, since there were only two blocks with the same composition as the low diversity plot. Additional site details can be found in Chapter 2.

3.3.2 Collection and identification

Specimens were collected between May and July 2016 using flight intercept traps and beat sheets. All samples were taken back to the laboratory for processing. All samples were sorted and separated into Coleoptera and non-Coleoptera. All specimens were identified and classified functionally with methods described in Chapter 2. We then determined functional and morpho species richness as well as abundance at the different plots and for each sampling period.

3.3.3 Structural Equation Modeling

We built the Sardinilla plantation model based on information from previous publications from the Sardinilla plantation and several ecosystem functioning and herbivory studies from other tropical sites, combined with the beetle data described in Chapter 2. Different models were tested in R to determine which one would best fit the data (Beaujean 2014). The additional models used the same set of variables (both latent and indicators), but with different configurations. However, the models were limited by the theoretical framework, which will be presented in the next paragraph. While the direction of the relationships could be moved around, it made noticeably little biological sense. Therefore, the model presented here is one that both works statistically and makes the most biological sense.

A visual representation of the model, shown in Figure 1, provides the framework for this research. Based on this model, I hypothesize that aboveground biomass will influence both Coleoptera diversity and canopy openness. Higher aboveground biomass would translate into higher resource availability for beetle herbivores (Hooper et al. 2005). In terms of canopy openness, higher aboveground biomass is likely to translate into higher leaf production, closing the canopy proportionally (Lovett et al. 2002). I then hypothesize that beetle diversity will influence levels of herbivory, which can translate to decrease in leaf mass and nitrogen content. We know that insect outbreaks can increase the loss of foliar nitrogen (N) and that this loss can then leach into the ecosystem and reduce longterm forest production (Swank et al. 1981; Webb et al. 1995; Eshleman, Morgan, and Webb 1998; Reynolds, Hunter, and Jr 2000). In terms of the leaf area, it has been shown that most of the leaf area loss in tropical forests is caused, either directly or indirectly, by leaf-chewing herbivores (García-Guzmán and Dirzo 2004; Ribeiro and Basset 2007). Since herbivore damage has been shown to influence ecosystem processes such as light penetration to the forest floor (Stephens, Turner, and Roo 1972; Campbell and Sloan 1977; Houston, Parker, and Wargo 1981; Lovett et al. 2002), the levels of herbivory should be reflected in the canopy openness. Then, if higher tree diversity promotes higher biomass and productivity,

I hypothesize that the crown volume of trees will also increase, translating into higher photosynthesis rates and higher C uptake (Murphy et al. 2008). Therefore, biomass should influence canopy openness. In terms of photosynthesis, I hypothesize that canopy openness will affect above ground C uptake, which, in this case, is used as a proxy for plot wide photosynthetic rate (Murphy et al. 2008).

In SEM, we can account for parts of the model we cannot directly measure. Therefore, we set these components as latent variables and use several indicators, variables that we can actually measure, to estimate the latent ones (Shipley 2000). Our model included two latent variables: Herbivory and Coleoptera diversity. For Herbivory, indicator variables were leaf mass area (LMA), specific leaf area (SLA) and leaf nitrogen content (LNC). Since I did not have measures of leaf damage due to herbivory, I chose leaf functional traits that would likely correlate with their susceptibility to herbivory and palatability to insects. For Coleoptera diversity, indicator variables were both abundance and functional diversity of beetles from the different plots.

In order to judge model fit, I used parameter estimates built into the **lavaan** package (Rosseel 2012) in R 3.1.1 (R Development Core Team 2015) such as RMSEA, CFI and TLI. We also performed an ANOVA to compare the two models that were built. We had to fix the variation of both functional diversity and Coleoptera abundance to be higher than 0. The **lavaan** package is not immune to returning negative variance when it is not possible with the data (e.g. when the values are not and cannot be negative) (Rosseel 2017). We tested both pooled and unpooled sampling period models. By performing an ANOVA, I could determine which one had the strongest support.

3.3.4 Data Collection

Specific leaf area (SLA) (cm²/g) (Salisbury and Potvin 2015) and leaf nitrogen content (LNC) (gN/kg) measures (Oelmann et al. 2010) were taken from previous studies in Sardinilla. In particular, specific leaf area (SLA) reflects leaf mechanical

properties that directly affect leaf palatability for insects and correlates with a number of other leaf traits that determine tissue quality for herbivores (Reich, Wright, and Cavender-Bares 2003; Wright et al. 2004). Rapidly growing species usually have higher SLA compared to slow-growing species (Wilson, Thompson, and Hodgson 1999). However, SLA demonstrated weak relationships with growth rates of woody plants in the tropics (Wright et al. 2010).

LNC units were multiplied by 10 in order to keep all variance at the same scale and be able to run the model in R. Leaf-mass area (LMA) (g/cm²) was measured by Marina Duarte (unpublished data) in the summer of 2016. The units were divided by 1000 in order to keep all variance at the same scale and be able to run the model in R. Above-ground carbon uptake was computed from Potvin et al. (2011). Canopy openness was computed using the GLA software (Frazer and Canham 1999) from hemispheric photographs taken in the summer of 2016. Biomass was computed using equations linking biomass, basal diameter, DBH and tree height from previously published work. Basal diameter, DBH and tree height measures are taken each year in the Sardinilla plantation and are stored in a database (Daniel Lesieur, unpublished database). I determined, by using species code in the database, the trees that were still alive in each plot. Then, I averaged and weighted the measures in terms of the corresponding tree's abundance in each plot. The measures were then used to build a SEM model using the lavaan package in R (Rosseel 2012; R Development Core Team 2015). I then visualized the model using the **semPLot** package in R (Epskamp 2013). While the data was mostly complete, there were some missing values, especially for the 9 species plots. While those missing values depended on the measure, I decided to keep each sampling period and the model treated the missing variable as 0.

3.4 Results

We performed an ANOVA to compare the pooled and unpooled model. It was clearly shown that the second model was a better fit to the data (Table 3.1) and it was therefore used for the rest of the analysis. The models were also tested against other theoretical models as explained earlier, but this unpooled model fitted better empirically and fitted the theoretical framework. In model fitting, we can compare a baseline (null) model against our fitted model to calculate relative indices of model fit. This baseline model, in which observed variables cannot covary with other variables, is considered the worst fitting model within the realm of reasonability for your data. The chi-square statistic tests perfect model fit, for both the specified and baseline model, using variance/covariance matrices. The chi-square value for our model (p=0) allows us to disregard the null model and accept our fitted model in terms of quality. Unfortunately, the Comparative Fit Index (CFI) (=0.521) and the Tucker-Lewis Index (TLI) (=0.211) are not strong. Additionally, the Root Mean Square Error of Approximation (RMSEA) (=0.264 (0.230-0.299), p=0.) is quite high and the standard deviation is quite large. All of these indices indicate poor model performance (Hu and Bentler 1999; Little 2013; Brown 2014; Kline 2015). While the model could have been corrected to try and improve model fit, the organization of the relationships would not have made biological sense. Therefore, the model I used was the best fit. However, the weakness of the relationships might be indicative of problems within the data.

Even if the model does not provide the best fit, it can still be observed and I can explore the relationships it exposes. When looking at Fig 3.1, we get a clear idea of those relationships. All paths were significant, using Chi square statistics (Table 3.3). In terms of the strength of the effect of endogenous variables, computed here using R² (Table 3.2), the most extreme value was the amount of variance associated with the endogenous variable SLA (R² = 0.0008). As seen in the path coefficient, SLA had no effect on herbivory since its whole effect size was linked to its own variation. Another low variable was the Coleoptera morpho species richness (R² = 0.2573), which was also mostly linked to its own variation. On the other end of the spectrum, the path between functional and Coleoptera diversity was fully explained by the relationship between the two variables. This might have created a fairly skewed behaviour of the Coleoptera diversity latent variable because of the highly uneven indicator variables.

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Some of the most evident relationships are the two negative path coefficients in the main loop (Fig 3.1). Aboveground biomass had a negative effect on Coleoptera diversity (Est=-0.014, p=0.001), which, in turn, negatively correlated with herbivory (Est=1.082, p=0.072). While the path coefficients are low, they still suggest that herbivores play some role in this ecosystem and match the biological explanation. In terms of positive relationship, Herbivory then had a positive relationship with canopy openness, even though the path coefficient is relatively low. Aboveground biomass was somewhat weakly linked to canopy openness and in a positive way; contrary to what I predicted. Carbon uptake was also only weakly linked to canopy openness (Est=0.281, p=0) and positively, which in this context agrees with our predictions. While SLA was not an explanatory factor of herbivory at all (Est=0.003, p=0.778), LMA (Est=1) and LNC (Est=0.130, p=0) were deemed to be meaningful explanatory factors for herbivory. Standardized path coefficients and standard errors for all paths are also computed in Table 3.3.

3.5 Discussion

The objective of this research was to use SEM to assess relationships between environmental variable and beetles in an experimental neotropical agroforestry setting, and to provide some clues to underlying causal mechanisms in this system. The major findings of this exploratory analysis show that there is a negative relationship between aboveground biomass and beetle diversity and between beetle diversity and herbivory. Additionally, biomass seemed to be the most important determinant of herbivory, as defined in our study.

Since most measurements were rather general and not measured specifically for this study, this may help explain the high variation of the different variables and the ensuing poorly fitting CFI, TLI and RMSEA values. While the model may not be overly robust, it is still valuable to analyze some of the observations made during this study.

3.5.1 Biomass and herbivory

In this study, I observed species-specific responses to small-scale spatial heterogeneity in the plantation. This result could show that aboveground biomass accumulation is a response to changing levels of plant diversity (Scherer-Lorenzen, Bonilla, and Potvin 2007). Therefore, it can affect rates of productivity and of biomass accumulation (Scherer-Lorenzen, Bonilla, and Potvin 2007). Healy, Gotelli, and Potvin (2008) showed the importance of species identity in investigating biomass and their allocation to different parts of the tree. Since the tree species present in Sardinilla differ in functional traits, such as the ability to fix nitrogen (Tilman 1999), they can strongly influence ecological processes as well as susceptibility to herbivores (Lovett et al. 2002).

However, the fact that higher biomass would lead to lower beetle diversity is not intuitive. Since biomass increased with higher tree diversity (Stanley and Montagnini 1999) and should subsequently decrease herbivory damage. I argue that the relationship observed, although weak, is indicative of an underlying mechanism of the plantation. Specifically, though more resources are available, niches are also more abundant, and therefore individual taxa are less abundant. Consequently, increasing beetle diversity would correlate negatively with herbivory. It is logical to think that damage would be more evenly distributed and less targeted to a specific part of the tree. This result could provide explanations for the findings of Chapter 2 where beetle functional diversity was higher in high diversity plots. Lower path coefficients surrounding beetle diversity and herbivory might indicate that the plantation design is efficient at limiting herbivory. By using native species and combining them in the plots, I can argue that the niche differentiation has a strong enough effect to provide protection, maybe at the scale of the whole plantation (Huntly 1991).

The weakness of the relationship might result from our choice of leaf attributes for the latent variable Herbivory. While the literature supports the use of LMA as a proxy for herbivory (Schuldt et al. 2014), it would have been valuable to include more leaf functional traits in the analysis to better understand how herbivory is linked to beetle abundance in the plantation. We could have used traits such as leaf toughness, C:N ratio and water content (which is negatively correlated with herbivory) (Coley 1983; Kursar and Coley 2003; Agrawal and Fishbein 2006; Fine et al. 2006; Adams et al. 2011). However, since the measurements used in this study were gathered from other studies, I was limited in my choice of functional traits for the model. The weak relationships surrounding Coleoptera diversity might also be remediated by better sampling effort, in terms of both beetle communities and leaf functional traits.

3.5.2 Phenology

It would have been valuable to include phenological strategies of the different tree species since they lead plants to differ in their resource-use efficiency (e.g. CO2 and nitrogen) (Sobrado 1991; Eamus and Prior 2001). The primary consumers of plant biomass are insects, who will synchronize their life cycles with the production of new leaf tissues (Villalobos et al. 2013; Pezzini et al. 2014) at the beginning of the rainy season (Dirzo and Domínguez 1995; Healy, Gotelli, and Potvin 2008). While this is the period I sampled in, I was unable to sample continuously across the entire rainy season. Therefore, I might have missed some beetle groups that emerge later or changed activity levels during the season. Additionally, nutritional quality differs during leaf maturation and senescence. Levels of fiber, phenolics and tannins will increase, while nitrogen content decreases (Silva, Espirito-Santo, and Morais 2015), all leading to lower consumption of mature leaves (Janzen and Waterman 1984; Boege and Marquis 2005; Silva, Espirito-Santo, and Melo 2012; Neves et al. 2014).

While foliage quality and other bottom-up forces will have a strong effect on herbivory intensity (Coley and Barone 1996; Stiling and Moon 2005), the herbivore community composition and abundance is another factor influencing rates of leaf damages. Silva, Espirito-Santo, and Morais (2015) found that high leaf damage inflicted on young leaves could be related to selective pressures of insects. If I had sampled more extensively and taken measurements relating to phenology, I could

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have added it to the model. In this way, I could have had a better understanding of herbivore behaviour at the most vulnerable time for the individual trees. An interesting aspect is that herbivory damage can challenge the allocation of carbon to parts of the tree, since the tree will produce defensive compounds if under attack (Schultz and Baldwin 1982; Lovett et al. 2002). Therefore, it would have been relevant to treat carbon uptake as a latent variable and include many carbon concentration measures.

3.5.3 Scale of investigation

An important aspect to consider is the scale at which I built the model. Since herbivory is mostly localized (even when it results in defoliation), the woody structure of the tree remains alive. Additionally, when the trees are not killed by intense defoliation, the time required for substantial canopy recovery will only take weeks, rather than months or years (Lovett et al. 2002). While trees will have to reallocate their resources for the recovery, the effect is still localized and might not show up the plot level. Therefore, by treating the analysis at the plot level, I have not encompassed some of the more localized effects of herbivory that will affect the resource allocation of individual trees. These localized effects may not be strong enough to be observed at the plot level. Another reason to reconsider the analysis at the species level is that herbivory rates will force trees to differ in their chemical defense levels and vary depending on their surroundings. Therefore, individual trees will react differently to new growing conditions and will allocate their resources accordingly (Basset 2003).

3.5.4 Recommendations

Based on our results, I provide the following recommendations for the modeling of beetle herbivores' influence on ecosystem functioning in agroforestry:

1. In order to provide a more complete picture of the plantation, sampling effort should be revised and increased. Not only should more trees be sampled, and more traps be used per plot, but other traps (such as Lindgren funnels traps) should be used to lessen bias in the taxa sampled.

- To gain a complete view of the beetle diversity in the plantation, more extensive temporal sampling should be done to capture leaf phenology. This strategy would be especially helpful in the context of herbivory since young leaves are more susceptible to it.
- 3. In terms of spatial scale, I recommend performing analysis at the individual tree level rather than at the plot level. Since herbivory is a rather localized process, it would be appropriate to consider localized effects of herbivory first, and then extrapolate to the plot, and finally to the plantation as a whole.
- 4. Using context specific ecosystem functioning measurements would improve the fit of the model. While the ones used in this study are valid approximations, they were not specifically taken during the study and might therefore not fit our theoretical assumptions perfectly.

3.6 Acknowledgments

We would like to thank Bill Shipley from Université de Sherbrooke for his help with the technical and theoretical construction of the model. We would also like to thank Daniel Lesieur for his help navigating the Sardinilla database. Special thanks to the members of the Buddle Lab (Chris Cloutier, Shaun Turney, Jessica Turgeon, Gail McInnis and Elyssa Cameron) for their ideas and support and to José Monteza and Lady Mancilla for their help on the field, in Panama. Financial support was provided by NSERC (BESS NSERC-CREATE Grant) and additional funding was provided by the Department of Natural Resource Sciences (McGill) as a Graduate Excellence Award, the National Science and Engineering Council of Canada (NSERC), in the form of a Discovery Grant to Chris Buddle and the Margaret DuPorte Fellowship. We also thank the staff at the Smithsonian Tropical Research Institute in Panama for logistical support.

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3.8 Figures and Tables

 Table 3.1 ANOVA values for the comparison of the two best fitting model constructed.

	Df	AIC	BIC	Chisq	Chisq diff	Df diff	P (> Chisq)
model.fit.2	17	1168,935	1187,736	29,052			
model.fit.3	17	7293,753	7346,703	182,895	153,8431	0,0000	0,0000

Table 3.2 R^2 values (proportion of variance explained) associated with each endogenous variable. Values are also seen in Figure 3.1

Indicators	R ²
func.div	1,0000
co.uptake	0,1464
coleo.abun	0,2573
LMA_1000	0,3193
SLA	0,0008
LNC_10	0,5932
canopy.open	0,2929
coleo.div	0,0796
herbivory	0,4251

Table 3.3 Parameter estimates for Latent variables, Regressions and Variances of the chosen model. Estimates refer to path coefficient estimates of the Structural Equation Model. These estimates inform us on the causality of the two indicators in the context of the whole model. In this case, I highlighted the two nonsignificant pathways.

		Estimate	Std.err	Z-value	P (> z)	std.lv	Std.all
Latent variables							
Colon div ==	coleo.abun	1,996	0,287	6,964	0	4,334	0,507
	func.div	1				2,171	1
	LMA_1000	1				14,003	0,565
Herbivory =~	SLA	0,003	0,012	0,282	0,778	0,047	0,028
	LNC_10	0,130	0,026	4,941	0	1,824	0,770
Degraceiene							
Regressions	borbiyory	0 222	0 000	2 622	0.000	2 246	0.200
Canopy.open ~	hiomass	0,232	0,000	2,022	0,009	0.027	0,390
	DIOITId55	0,037	0,022	1,070	0,094	0,037	0,202
Coleo div ~	biomass	-0 014	0 004	-3 479	0.001	-0 006	-0 282
	bioinace	0,011	0,001	0,110	0,001	0,000	0,202
	coleo.div	-1,082	0,602	-1,797	0,072	-0,168	-0,168
Herbivory ~	biomass	0,182	0,040	4,545	0	0,013	0,585
Co. uptake ~	canopy.open	0,281	0,057	4,9	0	0,281	0,383
	1						
	func.dv (vr.f)	0	0	105,58	0	0	0
		04 044	2 000	1	0	04 044	0.054
	CO.UPTK (Vr.C)	31,811	3,802	8,307	0	31,811	0,854
		04,212	60.0	0,307	0	04,ZIZ	0,743
	LIVIA_100	410,11	60,9	0,000	0	410,11	0,001
Variances:	SLA	2.860	0.342	8.364	0	2.860	0.999
	LNC 10	2.281	0.643	3,549	0	2.281	0.407
	cnpy.pn	48,924	6,563	7,455	0	48,924	0,707
	cole.dv	4,338	0,518	8,367	0	0,920	0,920
	herbvry	112,72	39,883	2,826	0,005	0,575	0,575
	-	5					



Figure 3.1 Visual representation of the Structural Equation Model. Square boxes represent latent variables and round boxes represent indicator variables. Arrows show the direction of the relationship.



Figure 3.2 Visual representation of the information presented in Tables 3.2 and 3.3 using the semPlot package in R. Circles represent latent variables and boxes represent indicators. Green arrows show positive relationships and pink arrows show negative relationships. In terms of strength o the relationship, weak relationships are represented by thin pale lines, mid-strength relationships are represented by dotted lines and strong relationships are represented by solid thick lines. The direction of the relationship is represented by the arrows. Indicator abbreviations read as follows: fn. = Functional diversity, cl. b = Coleoptera abundance, cl. d = Coleoptera diversity, bms = Biomass, hrb = Herbivory, cn. = Canopy Openness, LMA = Leaf mass area, SLA = Specific leaf area, LNC = Leaf nitrogen content and c.p = Carbon uptake.

Connecting Statement

The exploration of the data through Structural Equation Modeling in Chapter 3 provided a framework for future studies of beetle communities and ecosystem functioning through the effects of herbivory. While the model is not perfect, the results from this chapter go beyond the patterns I observed and provided complementary information to the patterns observed in the previous chapter. Both chapters suggest that stand diversification and its subsequent effect on beetle communities are efficient at reducing the harms of herbivory in agroforestry.

Findings from both chapters will be used in Chapter 4 to provide recommendations on future directions for studies pertaining to herbivory in sustainable agroecosystems in the tropics. This chapter will also summarize results obtained from previous chapters.

Chapter 4: Conclusions

This thesis establishes a solid foundational understanding of the effect of herbivory on ecosystem functioning in the Sardinilla plantation. Moving forward, the information gained from this project will add to the knowledge already accumulated by the Sardinilla project during the last 15 years. While the research at the plantation focuses mostly on biogeochemistry, this study provided an opportunity to link those abiotic processes to living organisms.

Chapter 1 established the context of the research. It focused on introducing insect herbivory and ecosystem functioning as well as the effect of stand diversification on ecosystem resilience. This was done in the context of reforestation initiatives and sustainable agroforestry systems in neotropical regions.

In Chapter 2, I discovered that stand diversification affects beetle communities, even at a small scale. This supports the body of work from Sardinilla, promoting stand diversification for reforestation initiatives. The results I obtained support the use of stand diversification as a means of reducing the potential harm caused by herbivorous beetles. While herbivores dominate the Sardinilla beetle community, patterns differ depending on the taxonomical and functional level. Additionally, I have provided further evidence of the importance of incorporating functional diversity into research and management initiatives, especially when thinking about ecosystem functioning. A high diversity of beetle functional groups suggests that the ecosystem is stable and resilient. This stability may be due to the use of native species in semi-natural density and composition, which provide inherent resilience to high herbivory rates. The results presented in this chapter also highlight the impact of local environmental factors, such as canopy openness and vegetation cover, on beetle communities.

Chapter 3 explored the links between herbivory, beetle communities, and ecosystem functioning. I used SEM to assess relationships between environmental variables and beetles in an experimental neotropical agroforestry

setting. This analysis provided some information on the underlying causal mechanisms in this system. The exploratory analysis showed that there is a negative relationship between aboveground biomass and beetle diversity, and between beetle diversity and herbivory. Additionally, biomass seemed to be the most important determinant of herbivory, as defined in our study. The findings supported the hypotheses of this study as well as further investigation of herbivory and ecosystem functioning in neotropical agroforestry ecosystems

Future Directions

Ideally, future studies would include more orders of insects, as beetles are not the sole arthropod herbivores in tropical forest systems. It would be valuable to test similar relationships with different insect orders and groups to decipher if stand diversification is lowers overall herbivory or if this relationship is only present with beetles.

The model I developed in Chapter 3 yield valuable results. However, the strength of evidence for the modeled relationships could be improved with further study. Sampling effort should be revised and increased, not only in terms of sampling events and phenology, but also in types of traps used. Additionally, I suggest the analysis both at the individual tree and at the plot level to observe effects of herbivory at different scales. Finally, the use of more context-specific ecosystem functioning measurement would improve the fit of the model.

The results presented in this thesis provide insight into the drivers of beetle communities in agroforestry systems in the Neotropics, and their relation to stand diversification and ecosystem functioning. While our understanding of agroforestry ecosystems continues to increase, thanks in part to research at the Sardinilla plantation, there remain many unanswered questions. We must continue to invest research effort into these ecosystems in order to promote sustainable agroforestry, encourage reforestation initiatives, and, ultimately, to support the people whose livelihoods depend on the agroforestry industry.