ADVANTAGES TO TROPICAL TREE SPECIES RARITY: RICHNESS OF NATURAL ENEMIES ON SEEDLING LEAVES AND NEGATIVE DENSITY DEPENDENCE.

By

Bénédicte Bachelot

A THESIS

Submitted to
Michigan State University
In partial fulfillment of the requirements
For the degree of

MASTER OF SCIENCE

Forestry
Ecology, Evolutionary Biology & Behavior

2011

ABSTRACT

ADVANTAGES TO TROPICAL TREE SPECIES RARITY: RICHNESS OF NATURAL ENEMIES ON SEEDLING LEAVES AND NEGATIVE DENSITY DEPENDENCE.

By

Bénédicte Marie-Philippe Bachelot

The Janzen-Connell hypothesis (JC) is one potential mechanism to explain the maintenance of high alpha diversity of tree species in tropical forests, operating through differential pressure by natural enemies. Constraints on the populations of common species could arise from a greater diversity of natural enemies. The objectives of this work were to test the new interpretation of the JC, assess the variability of the negative density-dependence (a more traditional way to test the JC) over time, and to offer a new conceptual model of seedlings community abundance. By assessing damage patterns on leaves, as a proxy for natural enemy species, I was able to prove that seedlings of common tropical trees host a higher diversity of aboveground natural enemies than seedlings of rare tropical trees. I also found that this resulted in a disadvantage in common species due to higher mortality risk due to aboveground foliar damage. However, from a negative-dependence perspective, common species are more often advantaged compared to rare species. These findings bring support for our interpretation of the JC. I then developed the conceptual model to reunify this interpretation and the variability of NDD. This theoretical model predicts that seedling abundance will oscillate between being rarer and more common over ecological time. The results offer a different step in understanding high tree species diversity in the tropics.

This work is dedicated to my family who managed to continually support me throughout my entire Master from the other side of the Atlantic and Pacific Oceans. I would also like to dedicate this research to my “cohort family”, especially Rachael Eaton, and other friends for supporting and joyfully distracting me. Finally, the work is dedicated to Bruno Herault who first introduced me to Tropical Ecology.

ACKNOWLEDGEMENTS

My first appreciation goes to my advisor and mentor Dr. Richard Kobe, whose support and ecological knowledge taught me how to conduct research and push me to study tropical ecology further. Before starting my Master's I already knew I wanted to become a researcher, Dr. Kobe gave me a strong foundation of tropical ecology knowledge that I know will help me during my PhD and future career. I also would like to acknowledge Dr. Andrew Finley and Dr. Nathan Swenson whose insights respectively in statistics, and in tropical ecology were necessary for my work. Another big acknowledgement goes to Agnes and Alain Bachelot, my parents, for helping me with the mathematic aspect of my works.

I also acknowledge AgroParisTech, my French engineering school that allowed me to pursue my Master's program abroad at Michigan State University. I thank Michigan State's Forestry Department and Ecology, Evolutionary Biology and Behavior program, which not only financially supported me but which offered me great courses to develop my skills. Organization for Tropical Study and La Selva staff members were of great assistance during my fieldwork. I am immensely grateful to Ademar Hurtado Flores and Ralph Garcia Robleto, two Costa Rican technicians responsible for the long-term census whose knowledge of the tropics was more than helpful.

Additionally, I would like to thank Corine Vriesendorp who started the long-term study in Costa Rica with my advisor and allowed me to use her incredible dataset. Finally, I would like to thank my entire family and friends who constantly supported me.

TABLE OF CONTENTS

CHAPTER III – Amount of foliar damage predicts future seedling mortality in a wet tropical forest

Methods

Discussion

CHAPTER IV – Negative density-dependent mortality varies over time offering a rescue process for seedlings of rare species in a wet tropical forest

Methods

Results

Discussion

CHAPTER V – Tropical seedling abundance cycles, a conceptual model

From rarity to commonness, part A and B in Figure 4.1

From commonness to rarity, part C and D in Figure 4.1

APPENDICES

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

How is it possible to find 300 different species of trees in a single hectare (Valencia et al. 1994)? Ecologists have studied this question of amazing biodiversity in tropical moist forests for several decades. This question is important as understanding how species coexistence operates may allow us to better manage forests and preserve these rich biomes. A multitude of hypotheses have been proposed but none has been widely accepted. Among them is the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) (subsequently: JC). This hypothesis assumes that natural enemies (e.g. herbivores, pathogens and seed predators) are agents of density/distance-dependent seedling mortality, which could lead to species coexistence by favoring species patchiness. Later, Connell (1978, 1984); interpreted JC as a community compensatory trend mechanism Common species, which occur closest to adult trees and at higher conspecific density, should suffer from natural enemies more than rare species. Despite the importance given to natural enemies, few studies have examined them in the tropics. By better assessing the role of natural enemies in tropical forests, we may be able to better manage, conserve, and restore these ecosystems. Moreover, one of the first steps before understanding species coexistence is to better assess the transition between seedlings and young trees and the role played by natural enemies. This problem is not new and many ecologists are working on this issue, but to my knowledge, no studies have assessed JC from the perspective of a natural enemy richness. A more traditional view of JC is the "conspecific neighbor effect" on seedling mortality, or negative density dependence (NDD) that is acknowledged to play an important role in tropical community assemblage. Natural enemies traditionally have been thought to be the agent of NDD mortality, with a strong emphasis on aboveground herbivores. But recent studies found evidence that other belowground agents might be responsible for density dependent mortality patterns (Bever 1997, 2002, Bonanomi et al. 2005, Kardol et al. 2007, Van der Heijden 2008, Kulmatiski et al. 2008, McCarthy-Neumann and Kobe 2008, Mangan 2010). With this project, my main goals are to assess JC from the perspective of natural enemy richness, to investigate the impact of damage on mortality, to assess temporal variation of NDD, and to develop a conceptual model of tropical seedling demography, that combines seedling aboveground natural enemy richness and belowground agents of NDD.

The Janzen-Connell hypothesis

Based upon the “theory of pest pressure” (Gillett 1962) and Paine’s plant community hypothesis (1966), Janzen (1970) and Connell (1971) separately hypothesized that natural enemies could be the agents of the observed density and distance-dependent tropical seedling mortality, which in turn could promote tree species coexistence by favoring the recruitment of heterospecifics near adult trees. Later, Connell added a community compensatory trend (CCT) interpretation of JC; he speculated that common species would be at a disadvantage compared to rare species due to higher pressure from natural enemies (Connell 1978, 1984). Gilbert (2005) wrote a review of JC and summarized the important assumptions that were made by Janzen and Connell. First, natural enemies must have different effects based on the host seedling. Second, it is important that there is a great diversity of natural enemies with different host preferences. If these conditions are not met, all seedlings would suffer the same amount of damage and the mechanism would not promote species coexistence. Finally, both hosts and natural enemies must experience a higher density near adult trees, so that rare species must find a “natural enemy free spot” to survive, and heterospecific seedlings are able to survive near an adult where it is difficult for conspecific seedlings to stay alive.

JC is widely thought to be a potential mechanism that maintains high alpha tree diversity in the tropics. Many studies have examined this theory, but most focused on the density/distance dependence of tropical seedling mortality without identifying the specific agents responsible for it. Most of these studies found evidence for density- or distance-dependent mortality patterns (see review by Clark and Clark 1984, Harms et al. 2000, Gilbert et al. 2001, Terborgh, Pitman et al. 2002, Kobe and Vriesendorp 2011). While the majority found support for JC, others showed no evidence for density or distance-dependent mortality (Clark and Clark 1984). Differing density/distance-dependent mortality across species can partly explain why previous studies found differing results about density/distance-dependent mortality (Clark and Clark 1984). It has also been shown that if JC takes place, it would be occurring in early life stages when seedlings are more susceptible to natural enemies because of the very restricted number of leaves (Lambers et al. 2002, Terborgh et al. 2002) and non-lignified stems. Thus, studies may be missing evidence for the patterns, because they strictly used older individuals. A more recent study stressed the importance of differing species’ recruitment; not taking species’ recruitment into account might change the conclusion on whether or not there is a density/distance-dependent mortality pattern since differences in species’ recruitment can overwhelm a density/distance-dependent mortality pattern (Lambers et al. 2002). Differences in life history stages and species recruitments may explain why, until now, results concerned with JC are so variable. Yet, focusing only on the mortality pattern will not sufficiently support or contradict JC. The main point of this theory is that natural enemies are the agents of density/distance-dependent mortality. While examining the mortality pattern, one has to include damage observations and then compare rare versus common species and differences in mortality to show the implications for community structure.

Seedling pathology

The disease triangle is well-known in temperate plant pathology and was first introduced by Stevens in 1960. It shows that three conditions must be combined for a disease to appear: a host plant, a pathogen, and a favorable environment. Specific cases of this triangle are well-studied in temperate ecosystems and many agricultural or gardening approaches result from this knowledge. It is also at the origin of ecologically-based management strategies. A common example is powdery mildew; reducing humidity around plants may keep the fungus away (Jenkyn and Bainbridge 1978). Yet for more resistant spores, it may be necessary to also avoid shade. The most compelling evidence of the disease triangle is the Irish potato famine (1845-1846); the concordance of a pathogen *Phytophthora infestans*, a potato crop host with little genetic variation and wet weather with mild temperatures led to the destruction of most of the potato crop. Today, by taking into account the disease triangle, farmers design their fields such that humidity is greatly reduced, and by doing so the Irish potato famine disaster remains history. Tropical pathology has not been a widely explored field due to the high diversity of pathogens, despite good sources to identify natural enemies (Borror et al. 1976, Sutton 1980, Ellis and Ellis 1985, Barnett and Hunter 1998). By better understanding the role of natural enemies in tropical forests and their interaction with abiotic factors, we may be able to find new solutions to manage, conserve or restore these extremely high diversity biomes.

Seedling mortality

The disease triangle also can be applied to seedling mortality in tropical forest ecosystems. In this case, three conditions would be necessary for natural enemies to cause death: a susceptible host seedling, a natural enemy, and a favorable environment. The triangle shows how important it is to incorporate the three dimensions while assessing JC. Host seedlings and specific natural enemies can exist, but if the environment is not favorable for the natural enemies, they will not lead to seedling mortality, and JC process would not take place. Previous studies have already shown how important it is to incorporate abiotic environmental factors. Shade and moisture can increase seedling mortality (Augspurger 1984, Givnish 1999), but attributing these responses to natural enemies is more challenging. Assessing effects of abiotic factors typically focuses on a specific type of fungus or a narrow slice of the community (Gilbert 2005, Gilbert and Webb 2007). Moreover, these interactions may be more complicated than suggested. It has been shown that irradiance could also turn endophytes of *Diplodia mutila* into pathogens on the palm, *Iriartea deltoidea* (Alvarez-Loayza 2009). While these studies offer a good advancement in understanding the role of natural enemies, they focus on a reduced number of enemies and host seedlings without taking into account abiotic factors. The second important part of the disease triangle, yet unexplored, suggests the influence of interaction between characteristics of host seedlings and pathogens on seedling disease (

damage or mortality). Host preference characteristic of the enemies has been explored, but few specific fungi have been studied (see Arnold et al. 2001, Zhou and Hyde 2001, Augspurger and Wilkinson 2007, Gilbert and Webb 2007, Gilbert et al. 2008, Kluger et al. 2008). A more recent study showed that the life history of the seedling (the host) might be an important factor to consider; shade tolerance was negatively correlated with density dependence mortality (Kobe and Vriesendorp 2011). Thus, when studying seedling mortality, the abiotic environment, and the host and enemy characteristics must be considered.

Negative Density-dependent mortality

A traditional way of assessing JC has been to test the negative impact of conspecific neighbors on seedling survival. Soil pathogens ,part of seedling natural enemies, have been thought to play an important role in plant soil feedbacks (PSFs). Many studies suggested that PSFs were an important, but under-explored, mechanism of community structure (Bever 1994, Reynolds et al. 2003, Callaway et al. 2004, Ehrenfeld et al. 2005, Kardol et al. 2007, Kulmatiski et al. 2008). Like specific agents of density/distance-dependent mortality, specific agents of PSFs are still under-identified, even though they may play a more important role than aboveground natural enemies of seedling. A recent greenhouse study by McCarthy-Neumann (2008) showed that for 6 tropical species negative feedbacks were more likely due to chemical elements than specialist soil pathogens: pair-wise effects between soil modification by particular species and species-specific seedling performance occurred regardless of soil sterilization. Underground, density/distance dependence mortality agents seem to be chemical rather than aboveground natural enemies. Other research has provided evidence that pathogens (Mangan 2010), and mycorrhizae (Bever 1997, 2002, Bonanomi et al. 2005, Kardol et al. 2007, Van der Heijden 2008, Kulmatiski et al. 2008) were likely agents of negative density-dependent mortality. However, mortality by NDD can be as high inside as outside of enclosures (Hulme 1994a, 1994b, 1996). Thus, a clear separation between the effect of aboveground and belowground natural enemies on seedling mortality exists, but to my knowledge only few work has been done to separate the two effects (but see Brown and Gange 1989). In my Master's thesis, I will consider that NDD is the result of the sum of aboveground NDD (ANDD due to aboveground natural enemies) and belowground NDD (BNDD). Both of these effects could be consistent with a community compensatory trend (CCT) and promote species coexistence, as in Webb and Peart (1999) where seedlings of rare tree species suffered from lower NDD than seedlings of common species. Recent ones found that NDD enhances shade tolerance (McCarthy-Neumann and Kobe 2008) and abundance gradients (Comita et al. 2010). Hence, aboveground natural enemies and belowground NDD agents can act in similar or opposite directions. A possible explanation for differing result regarding NDD and CCT might result from the variability of NDD over time. Comita et al. (2010) linked conspecific effect on individual (NDD) and species abundance (sum of adult basal area) and found that rare species were at a disadvantage. However, they used only 5 years of data. One can imagine that the rare species at the time of the study will not necessarily remain rare in future years. Many studies acknowledge the importance of studying biological mechanisms within a temporal framework (e.g. Ewel and Hiremath 2005, Bardgette et al. 2005). Interactions between soil organisms and roots can change over short time (seasons), plants can modify nutrients availability which in turns affects soil population over ten to thousands of years (Bardgett et al. 2005). Longer time scales can involve important transformations of the environment but also plant evolution. Because NDD is due to a variety of agents (more likely belowground agents) that are highly dynamic, it is important to examine variability in the strength and direction of NDD over time.

With this project, I aim first to test JC from the point of view of aboveground natural enemy richness. Then, I endeavor to more fully assess how abiotic factors and life history traits impact aboveground natural enemy richness. Next, I will explore seedling mortality from first a damage perspective and then an NDD perspective, taking into account temporal variation. Finally, I intend to reconcile the mortality by aboveground natural enemy richness (Aboveground NDD) with mortality due to belowground agents (BNDD) in a new conceptual model.

LITERATURE CITED

LITERATURE CITED

Alvarez-Loayza, P., 2009. The role of pathogens in determining plant recruitment and distribution patterns in a western amazonian floodplain. PhD thesis dissertation submitted to the Graduate School-New Brunswick Rutgers, New Jersey.

Arnold, A. E., Z. Maynard, and G. S. Gilbert, 2001. Fungal endophytes in dicotyledonous neotropical trees: patterns of abundance and diversity. Mycological Research, 105, 1502-1507.

Augspurger, C. K., 1984. Seedling survival of tropical tree species – Interactions of dispersal distance, light-gaps, and pathogens. Ecology, 65, 1705-1712.

Augspurger, C. K. and H. T. Wilkinson, 2007. Host specificity of pathogenic Pythium species: Implications for tree species diversity. Biotropica, 39, 702-708.

Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt, 2005. A temporal approach of linking aboveground and belowground ecology. Trends in Ecology and Evolution, 20, 634-641.

Barnett, H. L. and B. B. Hunter 1998. Illustrated genera of imperfect fungi. Illustrated genera of imperfect fungi (Ed. 4). MacMillan Pubication, New York.

Bever, J. D., 1994. Feedback between plants and their soil communities in an old field community. Ecology, 75, 1965-1977.

Bever, J. D., K. M. Westover, and J. Antonovics, 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85, 561-573.

Bever, J. D., 2002. Host-specificity of AM fungal population growth rates can generate feedback on plant growth. Plant and Soil 244, 281-290.

Bonanomi, G., F. Giannino, and S. mazzoleni, 2005. Negative plant-soil feedback and species coexistence. Oikos 111, 311-321.

Borror, D. J., D. M. DeLong, and C. A. Triplehorn. 1976. An Introduction to the Study of Insects. Holt, Rinehart & Winston, New York.

Brown, V.K., and A. C. Gange, 1989. Differential effects of above- and below-ground insect herbivory during early plant succession. Oikos, 54, 67-76.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben, 2004. Soil biota and exotic plant invasion. Nature, 427, 731-733.

Clark, D. A. and D. B. Clark, 1984. Spacing dynamics of a tropical rain-forest tree - Evaluation of the Janzen-Connell model. American Naturalist, 124, 769-788.

Comita, L. S., H. C. Muller-Landau, S. Aguillar, and S. P. Hubbell, 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science, 329, 330-332.

Connell, J. H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298–312. In P. J. D. Boer and G. R. Gradwell, editors. Dynamics of numbers in populations. Centre for Agricultural Publication and Documentation, Wageningen, Netherlands.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non equilibrium state. Science, 199, 1302-1310.

Connell, J. H., J. G. Tracey, and L. J. Webb, 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain-forest tree diversity. Ecological Monographs, 54, 141-164.

Ehrenfeld, J. G., B. Ravit, and K. Elgersma, 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources, 30, 75-115.

Ellis, M. B. and J. P. Ellis, 1985. Microfungi on land plants. An identification handbook. Microfungi on land plants. An identification handbook. MacMillan Pubication, New York.

Ewel, J. J., and A. J. Hiremath, 2005. Plant-plant interactions in tropical Forests. In Biotic interactions in the tropics, Their role in the maintenance of species diversity. Cambridge University Press, Cambridge, UK.

Gilbert, G. S., K. E. Harms, D. N. Hamill, and S. P. Gilbert, 2001. Effects of seedling size, El Nino drought, seedling density, and distance to nearest conspecific adult on 6-year survival of Ocotea whitei seedlings in Panama. Oecologia, 127, 509-516.

Gilbert, G. S., 2005. Dimensions of plant disease in tropical forests. Biotic interactions in the tropics: their role in the maintenance of species diversity, Cambridge Press University, Cambridge, UK.

Gilbert, G. S. and C. O. Webb, 2007. Phylogenetic signal in plant pathogen-host range. Proceedings of the National Academy of Sciences of the United States of America, 104, 4979-4983.

Gilbert, G. S., J. Gorospe, and L. Ryvarden, 2008. Host and habitat preferences of polypore fungi in Micronesian tropical flooded forests. Mycological Research, 112, 674-680.

Gillet, J. B., 1962. Pest pressure, an underestimated factor in evolution. Taxonomy and Geography, London, Syst. Assoc. Publication, 4, 37-46.

Givnish, T. J., 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology, 87, 193-210.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre, 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature, 404, 493-495.

Hulme, P.E., 1994a. Rodent post-dispersal seed predation in grassland: magnitude and sources of variation. Journal of Ecology, 82, 645-652.

Hulme, P.E., 1994b. Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. Journal of Ecology, 82, 873-880.

Hulme, P. E., 1996. Herbivores and the performance of grassland plants: A comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology, 84, 43-51.

Janzen, D. H., 1970. Herbivores and number of tree species in tropical forests. American Naturalist, 104, 501-528.

Jenkyn, J. F., and A. Bainbridge 1978. Biology and pathology of cereal powdery mildews. In The Powdery Mildews, 283–321, Academic Press, London.

Kardol, P., N. J. Cornips, M. M. L. van Kempen, J. M. T. Bakx-Schotman, and W. H. Van Der Putten, 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs, 77, 147-162.

Kluger, C. G., J. W. Dalling, R. E. Gallery, E. Sanchez, C. Weeks-Galindo, and A. E. Arnold, 2008. Host generalists dominate fungal communities associated with seeds of four neotropical pioneer species. Journal of Tropical Ecology, 24, 351-354.

Kobe, R. K. and C. F. Vriesendorp, 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14, 503-510.

Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold, 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters, 11, 980-992.

Lambers, J. H. R., J. S. Clark, and B. Beckage, 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature, 417, 732-735.

Mangan, S. A., E. A. Herre, and J. D. Bever, 2010. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant-soil feedback. Ecology, 91, 2594-2603.

McCarthy-Neumann, S. and R. K. Kobe, 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. Ecology, 89, 1883-1892.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist, 100, 65-75.

Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay, 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology, 84, 2281-2291.

Stevens, R.B., 1960. Plant Pathology, an Advanced Treatise, Vol. 3. 357-429. In J.G. Horsfall and A.E. Dimond (eds.). Academic Press, New York.

Sutton, B. C., 1980. The Coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. The Coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. Kew, Surrey, England: Mycological Institute.

Terborgh, J., N. Pitman, M. Silman, H. Schichter, and V. P. Nunez, 2002. Maintenance of tree diversity in tropical forests. Seed dispersal and frugivory: ecology, evolution and conservation. Third International Symposium-Workshop on Frugivores and Seed Dispersal, Sao Pedro, Brazil, 6-11 August 2000, 1-17.

Valencia, R., H. Balslev, and G. Paz y Miño, 1994. High tree alpha diversity in Amazonian Ecuador. Biodiversity and Conservation, 3, 21–28.

Van der Heijden, M. G. A., S. Verkade, and S. J. de Bruin, 2008. Mycorrhizal fungi reduce the negative effects of nitrogen enrichment on plant community structure in dune grassland. Global Change Biology, 14, 2626-2635.

Webb, C. O. and D. R. Peart, 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology, 80, 2006-2017.

Zhou, D. and K. D. Hyde, 2001. Host-specificity, host-exclusivity, and host-recurrence in saprobic fungi. Mycological Research, 105, 1449-1457.

CHAPTER II

Common tree species host more aboveground natural enemy species than seedlings of rare tree species?

(A new facet of the Janzen-Connell hypothesis)

ABSTRACT

The Janzen-Connell hypothesis (JC) is one potential mechanism to explain the maintenance of high alpha diversity of tree species in tropical forests, operating through differential pressure by natural enemies. Constraints on the populations of common species could arise from a greater diversity of natural enemies. I evaluated this mechanism by assessing damage patterns on leaves, as a proxy for natural enemy species in 44 species. Species that were more common over the last 5 years had more diverse damage patterns than rare species after correcting for abundance, indicating that common tree species host a higher natural enemy richness. Additionally, natural enemy richness also increased with species shade tolerance. To my knowledge, this study is the first that shows natural enemy richness increases with species abundance of host species, offering support for a novel interpretation of the Janzen - Connell hypothesis.

INTRODUCTION

A central question in forest community ecology is: how can hundreds of different species of trees co-exist in a single hectare? A multitude of hypotheses have been proposed to explain species coexistence but the question remains unresolved (Chesson 2000). Among the most prominent of explanations of tree species coexistence is the Janzen-Connell hypothesis (Janzen 1970, Connell 1971)(JC), which proposes distance and density-dependent natural enemies have strong host preferences and disproportionately attack seeds and seedlings of common species near adult trees (i.e., a community compensatory trend or CCT per Connell et al. 1984), offering a stabilizing mechanism for species coexistence (Chesson 2000).

Numerous studies have documented patterns of distance and density-dependent seedling mortality (Clark and Clark 1984,, Kobe and Vriesendorp 2011), but few have identified particular agents causing such patterns (Gilbert and Webb 2007, McCarthy-Neumann and Kobe 2008).The few studies that have explicitly incorporated natural enemies have focused on the amount of damage, which generally increases with increasing conspecific density (Augspurger and Kelly 1984; Schuldt et al. 2010), but relationships with distance are less resolved (Augspurger 1984, Norghauer et al. 2010).

Strong host preference has been proposed as a necessary condition for natural enemies to constrain the populations of common species (Janzen 1970). However, natural enemies in the tropics target a wide range of hosts (Zhou and Hyde 2001), leading some studies to conclude that natural enemies could not be responsible for density-dependent mortality (Hamilton et al. 2010). However, lack of specialization does not mean that natural enemies do not have a strong host preference at a more local scale(Thompson 2005), and the Janzen-Connell mechanism could still be occurring. Furthermore, different plant species can share natural enemies but each association can result in different levels of damage (Zhou and Hyde 2001). Thus, greater damage on common seedlings relaxes the condition that natural enemies be strictly host exclusive.

Closely related species could provide equally suitable hosts for specialized natural enemies and thus could share natural enemies (Gilbert and Webb 2007). Coley (1983) is frequently cited as showing evidence that tree life history traits influence susceptibility to natural enemies (also see McCarthy-Neumann and Kobe 2008, Kobe and Vriesendorp 2011), but this study also suggests the importance of phylogenetic distances on survival. Similarly, other studies have confirmed the importance of looking beyond the notion of conspecific and heterospecific species in understanding negative density dependence (Strauss et al. 2006). Phylogeny may be successful at predicting functional traits but abiotic conditions can heavily influence those traits, which in turn will influence natural enemies. Thus, abiotic factors have to be considered when looking at plant natural enemies.

Little research has, however, been conducted in the tropics to understand the effects of abiotic environmental conditions on natural enemies even though the disease triangle (a suitable host, environmental conditions, and presence of the natural enemy) is well established in temperate systems. Some studies suggest that damage decreases at high irradiance (Augspurger 1984), while other studies found that an increase in irradiance can increase damage by natural enemies (Alvarez-Loayza et al. 2008). The effect of abiotic factors may vary with traits of the host species; for example, drought may increase vulnerability to natural enemies in drought-intolerant but not drought tolerant species. The nature of the host also plays an important role as different species invest in different strategies. Fast-growing and pioneer species are thought to invest significantly in growth and little in defenses(Coley et al. 1985). In contrast, slow-growing shade tolerant species are thought to invest more in defenses, because loss of tissue is more costly to replace in the low light environments in which shade tolerant species often occur (Coley et al. 1985). Furthermore, environmental conditions affect plant traits (Wright et al. 2004), which in turn can influence the response to natural enemies (Fine et al. 2004). A tree species may develop a stronger tolerance to damage when growing in a favorable environment, whereas tolerance can be diminished when growing in a non-favorable environment (Fine et al. 2004). Therefore, it is important to consider natural enemies in the context of abiotic and biotic conditions.

In this study, I test the hypothesis that common seedling species host a higher diversity of aboveground natural enemies that in turn may lead to a disadvantage. Because of the large number of potential natural enemies, damage patterns were used as a proxy for natural enemy species (Currano et al. 2010). I predicted a higher species diversity of foliar natural enemies: 1) hosted by common species 2) when a species has lower average distances to conspecific trees 3) when a species on average has lower phylogenetic distance between neighboring individuals, 4) with decreased species shade tolerance, and 5) with higher average soil fertility and moisture conditions experienced by the species. Finally, I hypothesized that 6) a higher species diversity of foliar natural enemy would lead to an increase in foliar damage.

METHODS

Site Description

This project was conducted at La Selva Biological Station in the Atlantic Lowlands of Costa Rica (10º 26’N, 84º 00’ W). The core data set consists of five 1 x 200 m belt transects which were established across a soil gradient representative of major soil types: three transects on residual soils, one each on older and recent alluvial soils. All newly germinating and surviving woody seedlings have been surveyed in 1000 1-m^2 plots systematically every six weeks since 2000 (Kobe and Vriesendorp 2011). Liana and small palm seedlings were excluded here because adults were not mapped. All trees (> five cm diameter) within 20 m of the seedling quadrats were mapped and identified.

Damage patterns

From 13-22 January 2010, I took photos of every leaf on all seedlings within each of the five transects (a total of 869 seedlings of 113 species). A waterproof white sheet of paper was used as background. Based on the photographs, damage patterns were visually assessed for each seedling and differentiated using the following criteria: 1) position of the damage (e.g., edge or middle of leaf, proximity to principal vein), 2) shape of the damage (rounded, linear cut, regular), 3) size of the damage, 4) color (especially relevant to disease and pathogens) and 5) other defining characteristics (cut through veins, penetration through leaf or superficial grazing) (Figure A.1, Table A.1).

Categorical foliar damage

During each census from May 2008 to December 2010, damage on each seedling was evaluated and reported as a categorical variable representing the percentage of leaf damage. To validate the categorical observations, pictures of each leaf were taken in January 2010 to calculate the leaf area damaged area using WinFolia. Then, the photo estimates were compared with the categorical observation (r^2=0.7). Average damage experienced by each species was calculated over the censuses of 2008 (six months from May 2008 to December 2008).

Community, abiotic and biotic factors

To understand which factors potentially influence the number of damage patterns, a proxy for natural enemy richness, I measured community, abiotic and biotic factors (Table A.2). Seedling abundance for a species was assessed as the mean density of seedlings per m^2 during the sampling period. Abundance of tree species was assessed as the average number of conspecific trees within a radius of 20 meters around each seedling of the species, a typical neighborhood distance as estimated by Kobe and Vriesendorp (2011). The sum of tree basal area was used as a second proxi for species abundance at the tree stage. Distance from parent tree was assessed as the average distance from the closest adult tree.

To examine if past seedling species composition influenced natural enemy richness, I calculated and tested if seedling abundances over the past cumulative one, two, three, … nine, ten years were correlated with natural enemy richness.

To estimate effects of abiotic factors on enemy richness, I used previous measurements of canopy openness and soil resource availability (N, C, P and base cations) (Holste et al. 201_) to calculate the mean resource conditions experienced by each species. Soil moisture was measured every ten meters and was linearly interpolated to estimate the soil moisture for each seedling plot. Finally, I measured atmospheric humidity at 1 meter height along the transects five times during April 2010.

Using seedling mortality models (Kobe and Vriesendorp, 2011 and unpublished data), I calculated mortality under 1% irradiance to represent species shade tolerance. Previous studies stressed the importance of quantifying the ages of leaves when assessing damage because of an accumulation effect (Lowman 1984). To take this into account, I used the lifespan of each individual seedling to calculate the average lifespan of the seedling of each species, recognizing that seedling lifespan is a coarse approximation of leaf lifespan.

Phylogenetic analysis

Using a phylogenetic tree constructed in Phylocom (Webb et al. 2008), I calculated a matrix of phylogenetic distances between seedlings of all species present in the transects using the package Picante for R. I used an angiosperm base tree available with the newest version of Phylocom that gives ages for the nodes of the tree according to Wikstrom et al. (2001). Subsequently, I calculated the average neighborhood phylogenetic distance for each species known as the mean pair-wise phylogenetic distances method; for each individual *i* of a given studied species *s*, I averaged the phylogenetic distances between the individual *i* and all the seedlings j present in the same one m^2 quadrat. Then, I averaged the distances among individuals of the species s.

$$dp_X = \sum_j \sum_i (phylogeneticDistance)_{ji} \qquad \text{(Eq. 1)}$$

One hundred fifty-three individuals from 50 different morpho species, representing 12.5% of the total number of seedlings in the transects, were removed from the analysis because they were identified to the genus level solely. As for seedling abundance, I calculated the neighbor phylogenetic indices over different time periods: from the current time of the census to the past ten years.

Statistical analyses

I used R-project computing software (http://www.r-project.org) to perform all data analyses. Rarefaction curves allow comparing diversity estimates drawn from different sample size data. Thus, for each species, I developed rarefaction curves by calculating the cumulative number of different damage patterns when increasing the number of seedlings sampled using all possible combinations of sampling order.

I then fit a Michaelis-Menten function to the cumulative damage pattern for each species:

$$Nd_{i,s_i} = \frac{Nd_{\max,i} s_i}{K_i + s_i} \qquad \text{(Eq. 2)}$$

Where Nd_{i,s_i} is the cumulative number of damage patterns found on seedling species *i* for s_i seedlings. . $Nd_{max,i}$ is the asymptote of the curve and represents the expected total number of natural enemies hosted by the tree species *i*. K_i is a constant, which corresponds to the number of seedlings sampled to get to half the number of natural enemies hosted by the tree species (half of $Nd_{max,i}$) (Figure A.2). Models were fit for each species through minimization of sum of squared errors.

To test the factors that influence natural enemy richness across host species (the "community model"), I tested for relationships between $\mathrm{Nd}_{max,i}$ and potential factors (Table A.2) using linear and non-linear regressions. First, regression was realized for a subset of 30 species because of missing values for some of the factors. The best models were selected per Akaike information criterion (AIC). To estimate parameters, the model was then fit to all the species with values for factors selected by AIC in the first round of modeling. The set of best models was evaluated by AIC and r^2. The robustness of the best community model was assessed using a leave-one-out cross validation; the model is fitted using N-1 species and the Nth species is then predicted. This is repeated 29 times in order to get an estimate of natural enemy richness for each species.

To examine within-species variation in natural enemy species load, I used a similar regression approach for all species with >20 seedlings. The number of natural enemy species found on individual seedlings was modeled as a linear regression using the same abiotic and biotic factors as the community level model, but measured at the individual level rather than mean values for a species.

Finally to test if a higher diversity of foliar natural enemy species leads to a disadvantage, we performed a linear regression between Nd_{max} and amount of leaf damage experienced in 2008.

RESULTS

Within species

For each of the 44 species with $\geq$ three seedlings (see Table A.3 and Figure A.3), the cumulative number of natural enemy species increased less than proportionately with increasing numbers of seedlings sampled. No tree species reached asymptotic levels of enemy richness. Nevertheless, the Michaelis-Menten function provided good fits to the data, and provided estimates of both the maximum number of natural enemies (Nd_{max}) and the number of seedlings for half Nd_{max} (k) (Gottelli and Colwell 2001). The average fit of the model, using the square of the Pearson correlation, was $r^2 = 0.63$ with a range from 0.333 to 0.94, and was above 0.50 for 34 of 44 species.

I also tested for correlations between enemy richness and biotic and abiotic factors (13 different variables) at the individual seedling level for the five species with adequate sample sizes (N > 20). Among the five x 13 linear regressions, only four were significant, which is the experiment-wise expectation for significant results by random chance when the significance level is 0.05 for individual comparisons (Table A.4). Thus, I do not further discuss within-species results.

Across host species

I tested linear and non-linear effects on natural enemy richness by past host species seedling abundance and phylogenetic neighbor index (Table A.6 and A.7), and other abiotic and biotic factors. Because *Pentaclethra macroloba* had a very high abundance but a low foliar enemy richness, I considered it as an outlier and I removed this species from the analysis. Thus, I worked with 32 species (Figure 2.1, Table A.5). Under the best supported model, natural enemy richness linearly increased with conspecific seedling abundance over the past five years (AIC= 245, Table 2.1) and survivorship under 1% full sun (i.e., shade tolerance), and natural enemy richness increased as seedlings of a species tended to be near closely related individuals (as manifested by a negative relationship between natural enemy richness and current neighborhood phylogenetic index) (Figure 2.2 and Table 2.1). If natural enemy richness was strongly affected by host abundance, it was less sensitive to the neighborhood phylogenetic index, which was marginally significant. Sum of tree basal area, a proxy for adult abundance at the community level, was significantly positively correlated with aboveground natural enemy richness. However once the other factors were added, natural enemy richness was not significantly affected by sum of basal tree area. None of the interactions and the other abiotic and biotic factors significantly affected the load of natural enemies hosted by different species. Seedling abundance explained the greatest portion of the variability in Nd_{max} (0.417), followed by phylogenetic index (0.0649), and then shade tolerance (0.0581).

The data also supported models with non-linear increases of Nd_{max} with abundance (AIC=249, r^2=0.042-0.047, Table 2.1). As expected, host abundance positively affected natural enemy richness. However, the non-linear model was not supported once shade tolerance and the phylogenetic index were included.

The community model was simple; it made use of solely three factors and aggregated individual seedling variation to the species level. Yet, the models explained 55% of the variance of Nd_{max} across species. The model was also robust with respect to the leave-one-out cross validation method; leave-one-out estimates were correlated with observed natural enemy richness (linear model: r^2 = 0.39) (Figure A.4).

Sample size effect

If natural enemy richness increases with seedling sample size across species, the relationship between natural enemy richness and species abundance could be an artifact because I sampled more individuals of common species than rare species and sample size and long-term species abundance were positively correlated (r^2=0.45).

In order to verify that my estimates of enemy richness were not artifacts of seedling sample size, I randomly subsampled (with replacement) three individuals for each species in 1000 simulations. I then fit the Michaelis-Menten function to each species (consisting of three seedlings each) for each of the 1000 simulated subdata sets to obtain 1000 sets of estimated enemy richness for the focal species. For each of the 1000 simulated data sets, I fit the same linear community-level model of natural enemy richness versus explanatory factors. Natural enemy richness significantly increases with species abundance over the past 5 years and shade tolerance for each of the 1000 simulations. However, the phylogenetic index significantly decreases with increasing Nd_{max} for only 29% of the simulations, and it was marginally significant for 71% of the simulations. When only using the median, the lower and the upper boundary of the 1000 Nd estimates, I found that natural enemy richness significantly increased with both species commonness over the past five years and shade tolerance. It decreased as the genetic relatedness of the neighborhood decreases. However, this decrease in natural enemy richness was marginally significant when using the upper estimates of natural enemy richness (see Table A.8 and A.9). Overall, the significant relationship between Nd_{max} versus species abundance over the last 5 years and shade tolerance was robust to small sample sizes.

Nd_{max} and foliar damage

A total of 946 seedlings of 39 tree species were used. Higher natural enemy richness was positively correlated with the amount of damage experienced on average by a species in 2008 (Table 2.2, Figure A.5). The linear model successfully predicted the average amount of damage experienced by species in 2009 (r^2=0.64, p < 0.001).

DISCUSSION

Summary

Here, I extend the Janzen-Connell Hypothesis to species richness of natural enemies. foliar natural enemy richness increases with species abundance. I also found that species whose seedlings tended to occur near closely related seedlings had the highest diversity of natural enemies, consistent with my second hypothesis. However, contrary to expectation, shade tolerant species hosted more natural enemy species than intolerant species. Finally, I showed that an increase in foliar natural enemy diversity was positively correlated with an increase in foliar damage, suggesting a disadvantage for the species that host a high diversity of enemies.

Maximum number of natural enemies species was higher for common tree host species

Consistent with the first hypothesis, species that were more common at the seedling stage for the past 5 years hosted a higher diversity of natural enemies. This result is consistent with the CCT that predicts natural enemies should preferentially target seeds and seedlings of common tree species (Connell 1984). However, it is important to note that the abundance calculated at the tree stage was not a significant predictor of aboveground natural enemy richness in the final model meaning that aboveground natural enemy richness is more responsive to seedling abundance than adult abundance. Here, my results support this novel extension of JC and especially its negative density-dependent pattern but it is important to point out that I did not test whether a higher amount of damage results in a higher mortality rate. I am investigating those linkages in a related on-going study and preliminary results support a positive correlation among natural enemy richness, amount of damage ($r^2 = 0.64$), and mortality rate (Bachelot and Kobe 201_, in prep, also see Eichhorn et al. 2010). The strong difference in the number of natural enemy species hosted by common and rare species reinforces the potentially important role of natural enemies in creating and maintaining diversity (Janzen 1970, Fine et al. 2004).

The divergence of *Pentaclethra macroloba* from the general species relationship between natural enemy richness and species abundance could explain its dominance (Hartshorn, 1983) at La Selva. Its dominance has been interpreted to result from its high tolerance of infertile soil and a weak dry season (Hartshorn 1972), but my results suggest that its low number of foliar natural enemy species also could contribute to its high abundance. Leaves of P. macroloba seedlings are composite, with a high edge area ratio. Edges are less nutritious (Scriber and Slansky 1981), and are often avoided by herbivores. The leaves also close at night, offering fewer surfaces for herbivores, which are especially active at night (Elton 1973). The form and diurnal changes in *P. macroloba* leaves could explain its low diversity of foliar natural enemies.

Both current and past state of the community matter

The contemporary local seedling density observed in January failed to predict the maximum number of natural enemies. In contrast, the cumulative abundances of the host species over the past one to ten years were significant predictors of Nd_{max} with host abundance over the past five years as the best predictor. This may suggest a delay between species abundance and enemy richness response. Therefore, a longer-term assemblage of the community may be driving the natural enemy richness hosted by seedlings of different tree species. Although I cannot identify why a lag between abundance and natural enemy richness occurs, the lag does provide an opportunity for seedlings to become established after a mast event, ensuring the continued presence of the species in the community (Janzen 1974). If there was not a delay and density-dependent enemies responded almost instantaneously, then mast events would have no effect on seedling abundance (Silvertown 1980).

Species that tended to occur with seedlings of more closely related species had a higher enemy richness. This result was consistent with my third hypothesis; one may expect closely related species to share similar traits, and thus seedling species are unlikely to be distinguished by natural enemies. This finding is consistent with recent studies that proposed to expand the Janzen–Connell Hypothesis beyond the notion of conspecific and heterospecific (Webb et al. 2006, Gilbert and Webb 2007). The best predictors of natural enemy richness were current phylogenetic index and host abundance over the past five years, indicating that if seedlings of a tree species are common and genetically close to seedlings in the neighborhood, then it hosts more natural enemies than a seedling of a common species distantly related to the neighborhood. This is consistent with metapopulation theory (Hanski, 1999, Leibold et al., 2004) that predicts higher insect richness with larger and less isolated patches (Fenoglio et al, 2010). Over long temporal scales, specialist natural enemies may have time to target isolated common species that act as a food island (Strong et al. 1984, Novotny et al 2010), whereas at an immediate time scale highly related patches may attract more natural enemies especially generalists. However, I am not able to ascribe damage patterns to generalist vs. specialist enemies.

Nevertheless, the phylogenetic effect was relatively weak, perhaps because particular non-phylogenetically conserved functional traits were more important in influencing the interaction between the plant host and natural enemy; two closely related species can have very different morphological traits (Losos 2008). Traits involved in defense may not be genetically conserved (Agrawal and Fishbein 2006). Thus, trait distance rather than phylogenetic distance may better characterize the effects of neighboring individuals on a host's natural enemy richness. In addition, many species in my study were distantly related (on average, divergence from 40 million years ago), which decreases the power to detect a phylogenetic signal.

Natural enemy diversity was indifferent to distance from adult trees

According to JC, adult trees should act as a sink for natural enemies. Thus, I was expecting to find a higher diversity of natural enemies when the number of adult trees and the average distance from the closest adult were higher (Augspurger 1984). Unexpectedly, neither the mean number of adult trees nor the distance of the closest adult to the seedlings were important factors in predicting the maximum number of natural enemies hosted by a species (contrary to hypothesis 2). The lack of an effect probably was not due to lack of variation in mean distances among species, as distance ranged from three to more than 40 meters. However, the lack of a significant effect could have resulted from wide variation of distances to adults within species.

Ontogenetic shifts in leaf traits (Ishida et al. 2005) between seedlings and adults could lead to different ensembles of foliar enemies and a decoupling of adult presence / distance with seedling dynamics. In general, seedling leaves are thinner, have lower N and photosynthetic rates, and are less tough than adult leaves (Ishida et al. 2005). Since leaf traits between seedlings and adult trees are different, foliar enemies may also be different, consistent with the finding that both seedling and adult density can influence negative density dependence in seedlings (Kobe and Vriesendorp 2011).

Enemy richness increased with shade tolerance

Shade tolerance was negatively weakly correlated with natural enemy richness (r^2= 0.0581), contrary to expectations based on the correlation between defenses against enemies and shade tolerance (Augspurger and Kelly 1984, McCarthy-Neumann and Kobe 2008, Kobe and Vriesendorp 2011). The “defense-growth” hypothesis claims that shade tolerant species have slow growth and invest more resources in defenses than faster growing species. Shade tolerant species have tougher leaves (high leaf mass per area, LMA) and low nutrient content, making them less palatable for natural enemies (Coley et al. 1985, Kitajima and Poorter 2010). One potential explanation of this counter-intuitive result is that shade tolerant species may be better able to tolerate damage. Shade intolerant species, in contrast, may drop their leaves soon after experiencing damage. Nevertheless, other studies have shown that damage increases with shade (Augspurger 1984). If natural enemies prefer shaded environments, they may preferentially feed on the plant species that are more available in the shade. Shade tolerant species are also characterized by a long leaf lifespan (Kitajima and Poorter 2010), allowing more time for foliar natural enemies to accumulate. However, damage occurs principally as leaves are expanding (Lowman 1985), making an effect of leaf lifespan less likely.

Under the fourth hypothesis, I was expecting to find a higher diversity of natural enemies when on average a species occurs at higher total N content in the soil, since soil N often results in higher foliar N, which is preferred by herbivores (Mattson 1980). However, I found no effects of soil resources. The total N content in soil may not be a good predictor of the N content in leaves. Moreover, the type of N compound influences the behavior of herbivores; insoluble N compounds are not nutritious for insects (Scriber and Slansky 1981). Finally, N availibility influences the level of plant defenses (Coley et al 1985). Therefore, if a species experiences different N availability, this may create different levels of defenses that on average mask the effect of N on natural enemy richness.

A higher diversity of foliar natural enemy species lead to increasing damage

As hypothesized I found that high diversity of natural enemies leads to a greater amount of leaf damage. Richness of natural enemies may not necessarily correlate with the amount of damage, since a single enemy species can be extremely efficient at targeting its plant host (Botrell and Barbosa 1998). The positive relationship between natural enemy richness and the amount of damage indicates that hosting more enemies can lead to a disadvantage. One could argue that because I estimated the number of natural enemies from the number of damage patterns (Bachelot and Kobe 201_), my results could be an artifact of my methods. To account for this potential bias, I used the species level damage data from 2008 and 2009, while data from 2010 were used to estimate the number of natural enemies at the species level.

Caveats

Variation in seedling and leaf ages may introduce variability in the species-specific relationships between enemy richness and sampled seedlings. Seedings varied in age from 40 to 3579 days. Older leaves may accumulate more damage.

I did not explicitly include leaf traits in the community model of enemy richness. Inclusion of shade tolerance may have accounted for some variation in leaf traits due to covariance in shade tolerance and leaf traits (e.g., Kitajima and Poorter 2010). Several leaf traits have been shown to guard against herbivory; leaf mass /area is negatively correlated with herbivory (Currano et al. 2008, Kitajima and Poorter 2010), trichomes are avoided by herbivores (Levin 1973), and tannins and other leaf compounds make tissue less palatable to natural enemies (Coley 1983).

CONCLUSION

These findings add a new facet to the Janzen-Connell Hypothesis by demonstrating that common tropical seedlings host a greater number of natural enemy species than rare seedlings, which in turns lead to a higher amount of foliar damage. To my knowledge, this is the first study to test and find support for a relationship between aboveground natural enemy richness and tree species abundance at the seedling stage. The unforeseen finding that shade tolerance increased with the number of natural enemies hosted raises several new questions. For example, could this pattern be a consequence of a longer leaf lifespan for shade tolerant species? Or co-occurrence of both natural enemies and shade tolerant seedlings in the shade? Moreover, these findings reinforce the importance of going beyond the notion of conspecific and heterospecific species. This study adds a new dimension to density dependence mechanisms; not only does seedling mortality increase with conspecific density at a local scale (e.g., Kobe and Vriesendorp 2011), but I also found that the diversity of foliar natural enemies increases with conspecific density calculated at a broader scale (seedling abundance).

Table 2.1 Comparison of the different linear and non linear models when using different factors.

Model	Formula	Estimates (sd)				AIC	r^2 (%)
		i	a	b	c		
Linear	a*Abundance		15.23 (2.23)			299	60
Power	a*Abundance^b		38.02 (2.43)	0.21 (0.06)		258	35
Michaelis	(a*Abundance)/(b+Abundance)			n.s			
Linear	i + a*Abundance	27.96 (2.55)	6.16 (1.31)			249	42
Power	i + a*Abundance^b	22.80 (4.99)	13.14 *5.87)	0.61 (0.22)		249	47
Michaelis	i + (a*Abundance)/(b+Abundance)			n.s			
Linear	**i + a*Abundance + b*Shade_Tolerance + c*Phylogenetic_Index**	**46.83 (8.09)**	**5.75 (1.25)**	**-77.41 (28.85)**	**-0.11 (0.05)**	**245**	**55**
Power	i*Abundance^a + b*Shade_Tolerance + c*Phylogenetic_Index	29.27 (5.82)	0.33 (0.10)	n.s	0.09 (0.04)	257	39
Michaelis	(i*Abudance)/(a+Abundance) + b*Shade_Tolerance+ c*Phylogenetic_Index			n.s			

Table 2.2. Result of the regression between natural enemy richness and average amount of damage experienced by species

Factors	Estimate	Standard Error	t value	p value
Natural enemy richness	0.018406	0.002256	8.16	< 0.001

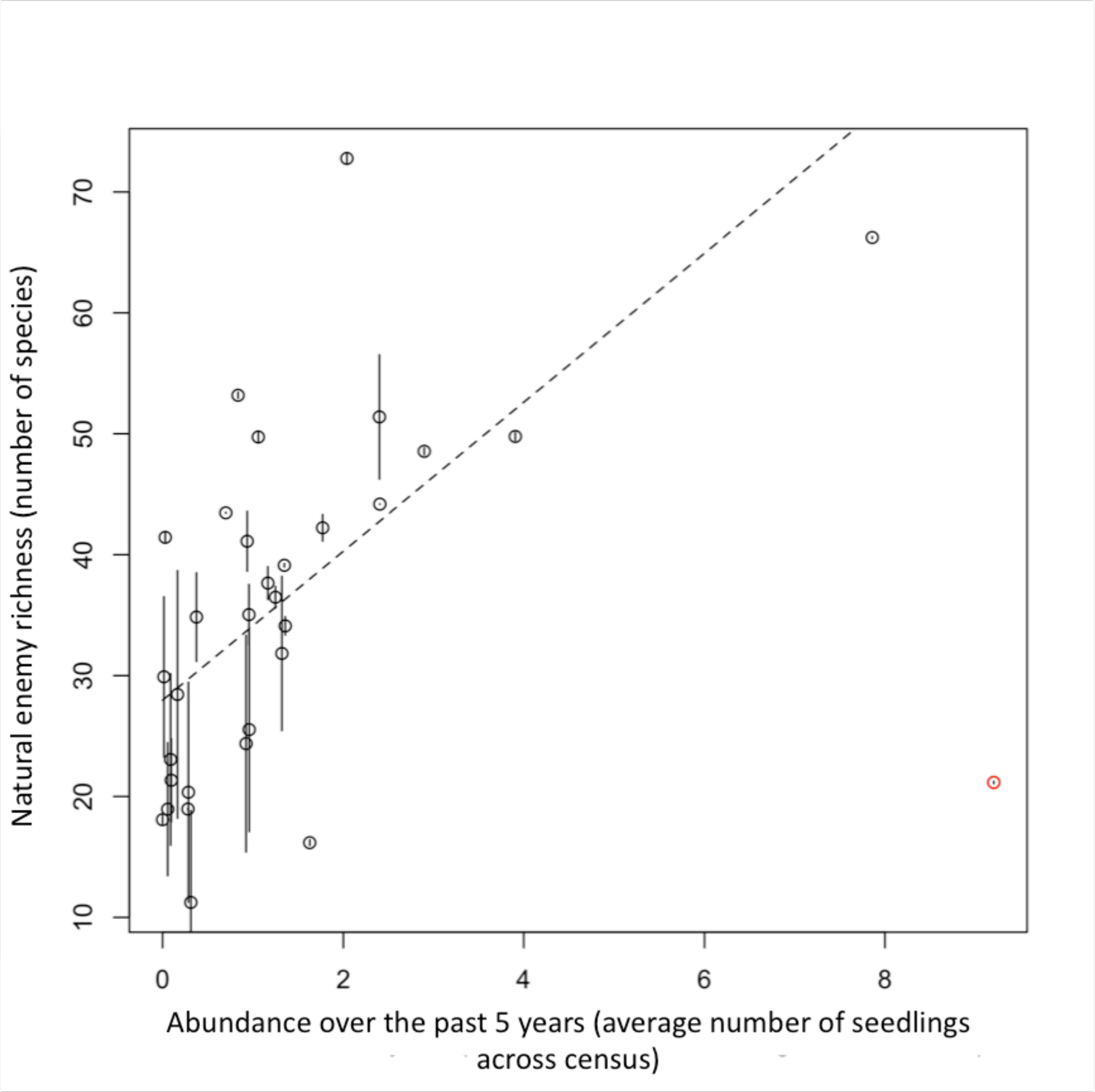


Figure 2.1. As the global abundance over the past 10 years increases, the number of natural enemy species increases. Vertical bars represent the 95% confidence intervals. *Pentaclethra macroloba* is the outlier in the lower right-hand corner.

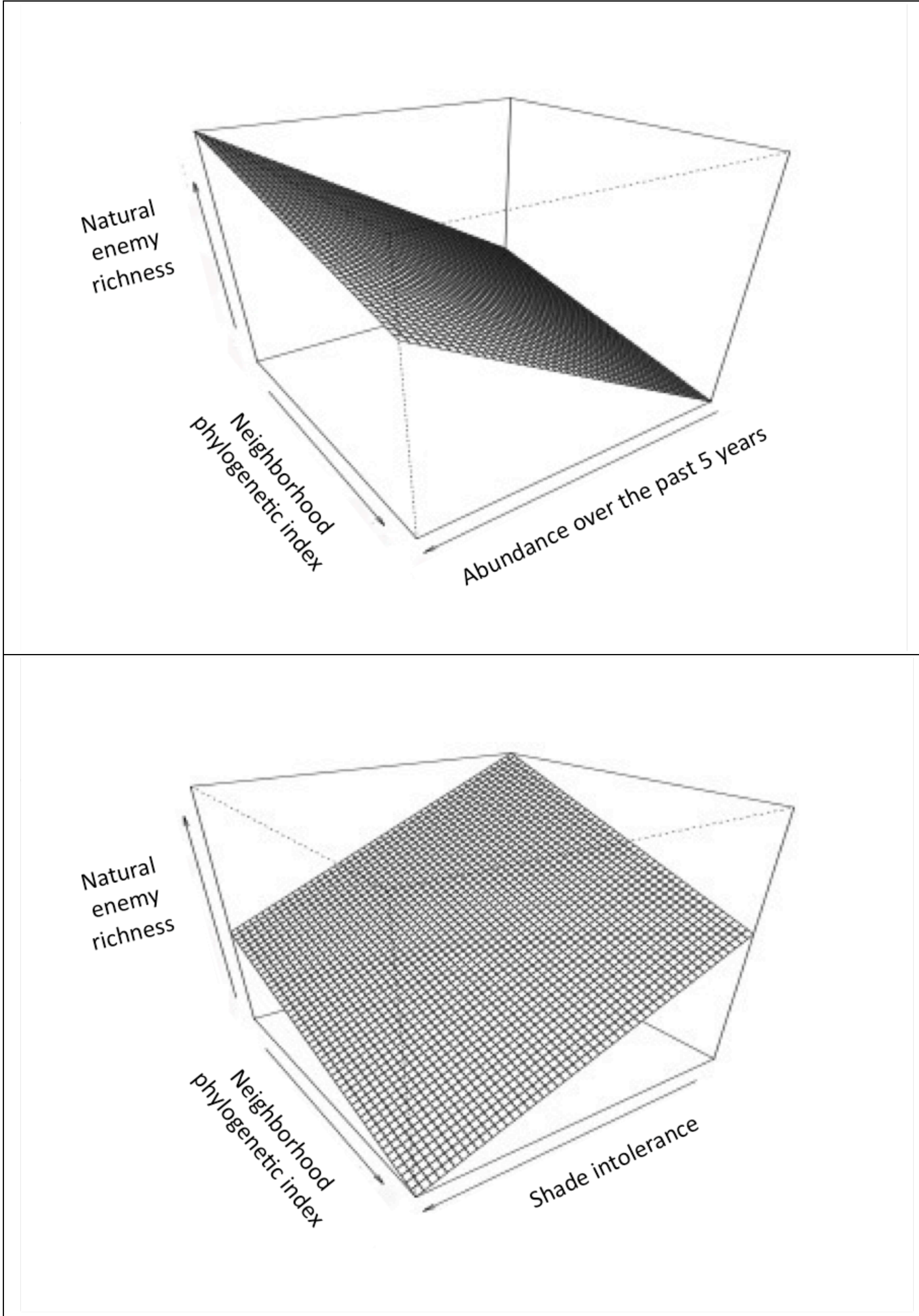
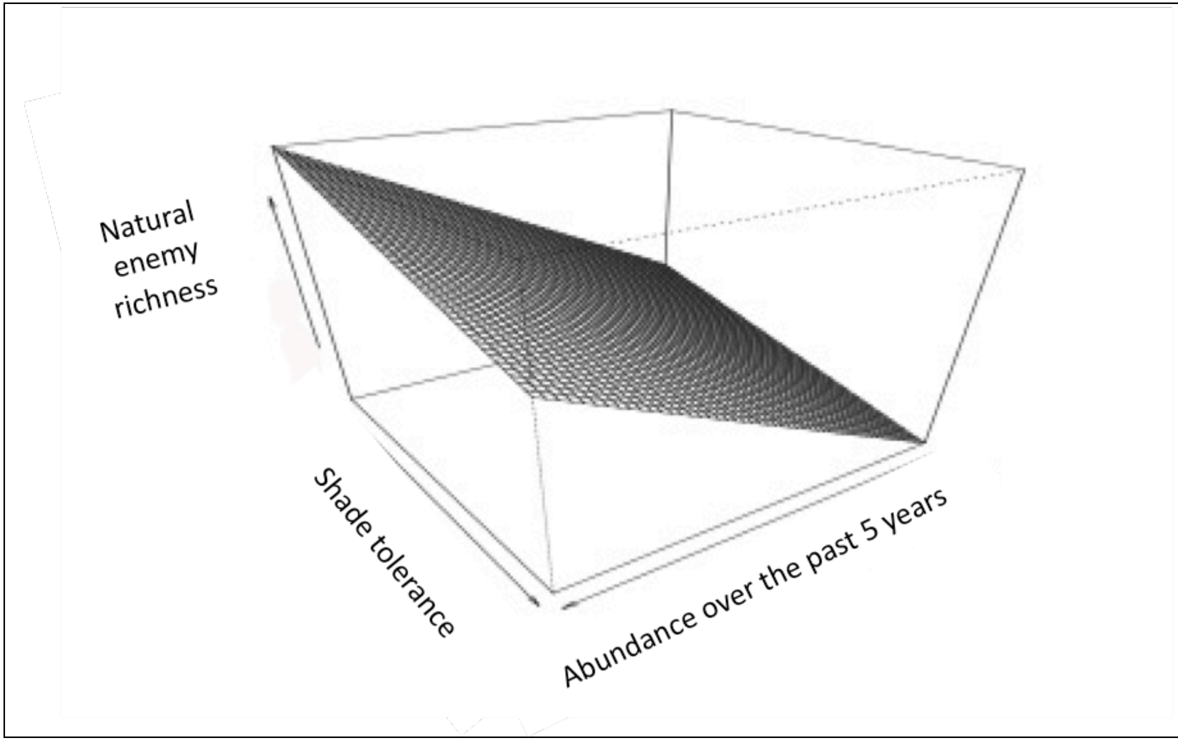


Figure 2.2. Predicted changes in natural enemy richness as a function of seedling abundance over the past 5 years, shade intolerance and neighbor phylogenetic index.

Figure 2.2. (cont’d)



.

LITERATURE CITED

LITERATURE CITED

Agrawal, A. A. and M. Fishbein, 2006. Plant defense syndromes. Ecology, 87, 132-149.

Alvarez-Loayza, P., J. F. White, N. Gil, J. C. Svenning, H. Balslev, and T. Kristiansen, 2008. Diplodia mutila causing seedling mortality of the palm Iriartea deltoidea. Plant Pathology, 57, 382-382.

Augspurger, C. K., 1984. Seedling survival of tropical tree species _ Interactions of dispersal distance, light-gaps, and pathogens. Ecology, 65, 1705-1712.

Augspurger, C. K. and C. K. Kelly, 1984. Pathogen mortality of tropical tree seedlings - Experimental studies of the effect of dispersal distance, seedling density, and light conditions. Oecologia, 61, 211-217.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343-367.

Clark, D. A. and D. B. Clark, 1984. Spacing dynamics of a tropical rain-forest tree - Evaluation of the Janzen-Connell model. American Naturalist, 124, 769-788.

Coley, P. D., 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs, 53, 209-233.

Coley, P. D., J. P. Bryant, and F. S. Chapin, 1985. Resource availability and plant antiherbivore defense. Science, 230, 895-899.

Coley, P. D., 1988. Effects of plant-growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia, 74, 531-536.

Connell, J. H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298 312 in P. J. D. Boer and G. R. Gradwell, editors. Dynamics of numbers inpopulations. Centre for Agricultural Publication and Documentation,Wageningen, Netherlands.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell, 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science, 329, 330-332.

Currano, E. D., P. Wilf, S. L. Wing, C. C. Labandeira, E. C. Lovelock, and D. L. Royer, 2008. Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum. Proceedings of the National Academy of Sciences of the United States of America, 1056, 1960-1964.

Eichhorn, M. P., S. G. Compton, and S. E. Hartley, 2008. The Influence of Soil Type on Rain Forest Insect Herbivore Communities. Biotropica, 40, 707-713.

Elton, C. S., 1973. Structure of invertebrate populatiopns inside neotropical rain-forest. Journal of Animal Ecology, 42, 55-104.

Fenoglio, M. S., A. Salvo, M. Videla, and G. R. Valladares, 2010. Plant patch structure modifies parasitoid assemblage richness of a specialist herbivore. Ecological Entomology, 35, 594-601.

Fine, P. V. A., I. Mesones, and P. D. Coley, 2004. Herbivores promote habitat specialization by trees in amazonian forests. Science, 305, 663-665.

Gilbert, G. S. and C. O. Webb, 2007. Phylogenetic signal in plant pathogen-host range. Proceedings of the National Academy of Sciences of the United States of America, 104, 4979-4983.

Gotelli, N. J. and R. K. Colwell, 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4, 379-391.

Hamilton, A. J., Y. Basset, and R. Tanese, 2010. Quantifying Uncertainty in Estimation of Tropical Arthropod Species Richness. American Naturalist, 176, 90-95.

Hanski, I. and M. Gyllenberg, 1997. Uniting two general patterns in the distribution of species. Science, 275, 397-400.

Hartshorn, G. S., 1972. The ecological like history and population dynamics of Pentaclethra macroloba, a tropical wet forest dominant and Stryphnodendron excelsum, an occasional associate. Ph. D. dissertation, University of Washington.

Hartshorn, G. S., 1983. Plants: Introduction. Costa Rican Natural History Ed. By D. H. Janzen, University of Chicago Press, Chicago, 118-157.

Holste, E. K., R. K. Kobe, A. O. Finley, and T. W. Baribault, 201_. Spatial heterogeneity of sol resources in a wet tropical forest. In prep.

Ishida, A., K. Yazaki, and A. L. Hoe, 2005. Ontogenetic transition of leaf physiology and anatomy from seedlings to mature trees of a rain forest pioneer tree, Macaranga gigantea. Tree Physiology, 25, 513-522.

Janzen, D. H., 1970. Herbivores and number of tree species in tropical forests. American Naturalist, 104, 501-528.

Janzen, D. H., 1974. Tropical black water rivers animals and mast fruiting by the dipteropcarpaceae. Biotropica, 6, 69-103.

Kitajima, K. and L. Poorter, 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. New Phytologist, 186, 708-721.

Kobe, R. K. and C. F. Vriesendorp, 2011. . Conspecific density-dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14, 503:510.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, and D. Tilman, 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7, 601-613.

Levin, D. A., 1973. Role of trichomes in plant defense. Quarterly Review of Biology, 48, 3-15.

Losos, J. B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, 11, 995-1003.

Lowman, M. D., 1984. An assessment of techniques for measuring herbivory - Is rainforest defoliation more intense than we thought. Biotropica, 16, 264-268.

Lowman, M. D., 1985. Temporal and spatial variability in insect grazing of the canopies of 5 australian rainforst tree species. Australian Journal of Ecology, 10, 7-24.

Mattson, W. J., 1980. Herbivory in relation to plant nitrogen-content. Annual Review of Ecology and Systematics, 11, 119-161.

McCarthy-Neumann, S. and R. K. Kobe, 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. Ecology, 89, 1883-1892.

Norghauer, J. M., J. Grogan, J. R. Malcolm, and J. M. Felfili, 2010. Long-distance dispersal helps germinating mahogany seedlings escape defoliation by a specialist caterpillar. Oecologia, 162, 405-412.

Novotny, V., S. E. Miller, L. Baje, S. Balagawi, Y. Basset, L. Cizek, K. J. Craft, F. Dem, R. A. I. Drew, J. Hulcr, J. Leps, O. T. Lewis, R. Pokon, A. J. A. Stewart, G. A. Samuelson, and G. D. Weiblen, 2010. Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. Journal of Animal Ecology, 79, 1193-1203.

Schuldt, A., M. Baruffol, M. Böhnke, H. Bruelheide, W. Härdtle, A. C. Lang, K. Nadrowski, G. von Oheimb, W. Voigt, and H. Zhou, 2010. Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology, 98, 917-926.

Scriber, J. M. and F. Slansky, 1981. The nutritional ecology of immature insects. Annual Review of Entomology, 26, 183-211.

Silvertown, J.W., 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society, 14, 235-250.

Strauss, S. Y., C. O. Webb, and N. Salamin, 2006. Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Sciences of the United States of America, 103, 5841-5845.

Strong, D.R., J. H. Lawton, and S. R. Southwood, 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific Publications, Oxford, U.K.

Thompson, J. N., 2005. The geographic mosaic of coevolution. University of Chicago Press, chicago.

Webb, C. O. and D. R. Peart, 2000. Habitat associations of trees and seedlings in a Bornean rain forest. J. Ecol., 88, 464-478.

Webb, C. O., G. S. Gilbert, and M. J. Donoghue, 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a bornean rain forest. Ecology, 87, S123-S131.

Webb, C. O., Ackerly, D. D., ans S. W. Kembel, 2008. Phylocom: software for the analysis of phylogenetic community structure and character evolution. Version 4.0.1. URL: http://phylodiversity.net/phylocom/

Wikstrom, N., V. Savolainen, and M. W. Chase, 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B-Biological Sciences, 268, 2211-2220.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, and M. Diemer, 2004. The worldwide leaf economics spectrum. Nature, 428, 821-827.

Zhou, D. and K. D. Hyde, 2001. Host-specificity, host-exclusivity, and host-recurrence in saprobic fungi. Mycol. Research, 105, 1449-1457.

CHAPTER III

Amount of foliar damage predicts future seedling mortality in a wet tropical forest

ABSTRACT

The Janzen – Connell hypothesis (JC) remains controversial in the tropics. My previous results indicated that seedlings of common tree species host a higher diversity of aboveground natural enemies than seedlings of rare tree species which in turns lead to higher amount of foliar damage. If foliar damage is correlated to seedling mortality, then my results bring support to the JC and a community compensatory trend (CCT) that seedlings of common species are constrained by natural enemies more so than rare species. Based on data from a long-term seedling census at La Selva Biological Station (Costa Rica), I found that young seedling mortality risk increased with increasing amount of leaf damage bringing support for CCT at the young seedling stage mediated through aboveground natural enemy diversity and leaf damage. However, the positive effect of damage on seedling mortality disappeared with seedling age suggesting that older seedlings are less susceptible to damage than young seedlings. Thus, strong density-dependent filters appear to operate most strongly at the earliest seedling stages.

INTRODUCTION

The Janzen – Connell model (JC) hypothesizes that natural enemies of seeds and seedlings are responsible for the high alpha tree diversity in tropical forests (Janzen 1970, Connell 1971). JC hypothesizes the natural enemies of seeds and seedlings to be distant from adult tree or density of conspecific seedling responsive. Therefore, they should promote the recruitment of heterospecific seedlings. Based on the recognition that seedlings of common tree species more often occur close to parent trees at high density, Connell proposed the idea of a community compensatory trend (CCT) (Connell 1978, 1984); that is, natural enemies should preferentially target seedlings of common species, therefore disadvantaging them compared to seedlings of rare tree species.

Seedlings of common species host a higher diversity of aboveground natural enemies than seedlings of rare tree species (Bachelot and Kobe 201_). Furthermore, common species on average suffered from a higher amount of foliar damage than rare species (Bachelot and Kobe 201_). However, this study did not test the consequence of hosting a high diversity of aboveground natural enemies on mortality. A previous study found that seedling leaf damage was a good predictor of future seedling mortality in the tropics (Eichhorn et al. 2010).

Ontogenetic shifts in leaf traits (Ishida et al. 2005) between seedlings and adults could lead to different tolerance to damage as seedlings grow older. In general, seedling leaves are thinner, have lower N and photosynthetic rates, and are less tough than adult leaves (Ishida et al. 2005). Therefore, young seedling may be more susceptible to damage than older seedlings. This idea has been proposed in a model of change in tolerance, ability to maintain fitness, to damage with ontogeny (Boege and Marquis 2005); once cotyledons reserves are depleted, the seedling becomes less tolerant but soon it develops defenses and tougher leaves, building up a tolerance (traits increasing the ability of a plant to reduce the impact of damage) to damage (del-Val and Crawley 2005). These ontogenic shifts in leaf traits and defense may be a critical covariate to understanding consequence of foliar damage on mortality risk.

In this study, I aim to test if 1) higher foliar damage increases seedling mortality risk, 2) older seedlings are less susceptible to damage than younger seedlings, and 3) common species have higher risk of mortality via damage than rare species.

METHODS

Site

This project was conducted at La Selva Biological Station in the Atlantic Lowlands of Costa Rica (10º 26’N, 84º 00’ W). The core data set consists of five 1 x 200-m belt transects which were established across a soil gradient representative of the landscape-level occurrence of major soils: three transects on residual soils, one on older alluvial soils, and one onrecent alluvial soils. All newly germinating and surviving woody seedlings were systemaically surveyed in 1000 1-m^2 plots every six weeks since 2000 (Kobe and Vriesendorp 2009). Liana and small palm seedlings were excluded from this study because adults were not mapped. All trees (> 5 cm diameter) within 20 m of the seedling quadrats were mapped and identified.

Damage and survival time

During each census from May 2008 to December 2010, damage on each seedling was evaluated and reported as a categorical variable representing the percentage of leaf damage. To validate the categorical observations, pictures of each leaf were taken in January 2010 to calculate the damaged leaf area using WinFolia. Then, the photo estimates were compared with the categorical observation, which were strongly correlated ($r^2=0.7$). Average damage experienced by each species was calculated over the censuses of 2008 (six months from May 2008 to December 2008). In order to test the relationship between amount of damage and survival, I used census data from 2009. The last status in 2009 of each seedling was evaluated as either dead (1) or alive (0). The amount of damage experienced by each seedling before its last census in 2009 was categorically recorded.

Species abundance

At the community level, seedling species abundance was defined as the sum of the basal areas of conspecific adult trees present along the five transects in order to test for a CCT.

Statistical analyses

To test if a higher amount of foliar damage leads to a disadvantage, I fit a mortality model using a Bernoulli distribution, whose probability of mortality at the last census (t) was inversely correlated to the inverse logit of the amount of damage experienced at the census before the last census recorded for the individual (t-1) and to the seedling's age at t:

$$\begin{aligned} &status_t \sim dbern(p_i)a \\ &p_i = \log it^{-1}(m + (s + a * \log(age_i)) * damage_{i,t-1}) \end{aligned} \qquad \text{(Model 1)}$$

I fit the parameters of interest, *m* (the mean probability of mortality with 0 damage), *s* (the increase in probability of mortality due to damage) and *a* (the interaction between age and damage of the individual), using a Bayesian framework. I assessed significance of the parameters with 95% credible intervals. The significance of the model was assessed using a Bayesian p-value that was calculated from the distribution of the difference between the simulated and expected difference between number of dead and alive seedlings. Convergence of the model was assessed using the Gelman and Rubin convergence criteria on two chains starting with over-dispersed initial values (Brooks and Gelman 1997). I used a non-informative proper prior for each of the parameters (dnorm (0,100)). The model was validating by simulating data from the model and re-estimating the posterior distributions of the parameters (Figure B.2). I also used the same model using the average amount of damage experienced by the individual before the last census.

Finally to directly test for differing probability risk across seedling species abundance, I use model 1 and added the effect of seedling age and the interaction between species abundance and damage (Model 2):

$$status_t \sim dbern(p_i)$$
$$p_i = \log it^{-1}(m + (s + a * \log(age_i)) * damage_{i,t-1} + b * \log(age_i) + e * \log(abundance_i) * damage_{i,t-1})$$

To test the models, I simulated data from the model, re-estimated the posterior distributions of the parameters using the simulated data and compared posterior distributions. Finally, I assessed the predictive value of the models via cross validation method by fitting 20% of the data using the remaining 80% to fit the model. I repeated this method 5 times to predict 100% of the data. Then, I compared the observed and predicted status of each individual.

RESULTS

At the individual level (Model 1), individual young seedlings had a higher risk of mortality due to increased amounts of damage (significant positive posterior for *s*) but this effect disappeared with seedling age (significant negative posterior for *a*) (Figure 3.1 and 3.2, Table 3.1). The mortality model 1 successfully described the status of individual seedlings at the next census, based on the amount of damage at the penultimate census (Figure 3.3 and Figure B.1, Bayesian p = 0.49). The fit of the model is consistent across damage categories suggesting that age and damage are good predictors for each individual (Figure 3.3). Age and damage of individual seedlings, disregarding of species identity, was able to successfully predict 64% of individual mortality when using cross-validation. However, the average amount of foliar damage experienced by an individual before the last census failed to predict the status of the seedling at the next census.

Mortality risk also increased with community species abundance, calculated as the sum of conspecific adult tree basal area (Model 2, Table 3.2, Figure 3.4). When taking into account the effect of seedling age (and not solely the interaction with damage), we were better able to predict dead seedlings (42% in Model 2 with and without the interaction between age and abundance versus 26% in Model 1).

DISCUSSION

Summary

I found that mortality of individual seedling could be successfully predicted by the age of the individual and the amount of damage disregarding of the species identity. My results indicate an increase in mortality risk associated with increasing damage. However, this result was true only for the youngest stage of seedlings reinforcing the importance of examining how demographic processes change over ontogenic time (Boege and Marquis 2005). Finally, I found that mortality risk was higher in more abundant species than in less abundant species supporting a community compensatory trend.

Higher diversity of natural enemies leads to a disadvantage for common species

I demonstrate that a higher amount of damage leads to a higher risk of mortality, which is consistent with Eichhorn et al. (2010). Previously, I found that high diversity of natural enemies leads to a greater amount of leaf damage (Bachelot and Kobe 201_). Thus, we can infer that seedlings of common species are at a higher mortality risk than seedlings of rare species. My results (Model 2) are consistent with CCT since species with higher adult sum of basal have a higher probability of mortality than less abundant species.

If a plant species has a strong tolerance to damage, then there may not be a relationship between damage and survival (Beck 1965, Mopper et al 1991, Cobb and Whitham 1993, Gehring et al. 1997, Parker and Gilbert 2007). Thus, linking damage and survival help to address the impact of damage at the community level by understanding which individual seedlings survive past the second demographic bottle necks (the first one being seed germination). Few studies have examined the effect of natural enemies on seedling survival. Most of these used insect enclosures to compare seedling survival and growth, documenting no significant differences in growth and survival outside and inside the enclosure, and failure to support JC (Augspurer 1984, Hulme 1994a, 1994b, 1996, Fine et al. 2004). However, the results of my study and previous research (Bachelot and Kobe 201_) support the hypothesis that natural enemies preferentially target common species and disadvantage them by increasing mortality risk that is consistent with CCT.

Older seedlings are less vulnerable to damage

The relationship between survival and amount of damage matched my expectation that high amounts of leaf damage led to a high probability of mortality, but solely for the youngest seedlings. Once cotyledon reserves have been exhausted, seedlings may become more and more tolerant to damage (del-Val and Crawley 2005). Damage has indirect negative effects on other non-damaged leaf area via chlorophyll depletion (Zangerl et al. 2002), decrease in photosynthetic activity in remaining tissue due to damage, thus once seed reserve is used, young seedlings may not be able to tolerate damage (Boege and Marquis 2005).

The change of the effect of damage on mortality with seedling age highlights the importance of considering ontogenetic change in seedling resistance (defense and tolerance) when testing the JC and the CCT; these theories place natural enemies and damage at the center of the process through increased damage and thus mortality in common seedlings. If the seedlings are old enough, then damage may not impact their probability of surviving and thus it will not influence the community structure, and I propose that other processes might become prevalent such as competition and interactions with abiotic factors (interactions with soil, see Fine et al. 2004). Therefore, my results are consistent with the JC and its CCT interpretation at the earlier life stages of seedlings. This result stresses out the importance of examining the youngest individuals when assessing the effect of aboveground processes when often studies use >1cm DBH individuals. My findings additionally implies that the aboveground aspect of NDD may not be the strongest community driver at the sapling and tree stages, and it may explain why previous studies fail to detect an effect of aboveground natural enemies on seedling mortality (Augspurer 1984, Hulme 1994a, 1994b, 1996, Fine et al. 2004).

CONCLUSION

This study tested the consequence of foliar damage and seedling age on seedling mortality. According to my hypotheses, high amount of foliar damage increases seedling mortality risk. Along with my previous study (Bachelot and Kobe 201_), this result brings support for both the JC and the CCT from an aboveground natural enemy diversity point of view. To my knowledge this is the first time that such an interpretation of the JC and CCT has been tested. This reinforces the importance of taking into account natural enemies when testing potential mechanisms for tree species coexistence in the tropics from a diversity point of view.

Table 3.1. Result of the posterior distributions for the mean probability of mortality, the damage effect and the interaction between damage and age effect (Model 1).

Estimates	**Mean**	**σ**
m	-0.9390	0.2041
s	1.2398	0.1956
a	-0.2352	0.0355

Table 3.2 Result of the posterior distributions for the parameters in Model 2 including the interaction between species abundance and damage.

Estimates	Mean	σ
m	1.5698	0.5024
s	-0.1544	0.0581
a	0.4618	0.3461
b	-0.3641	0.0985
e	0.0338	0.0242

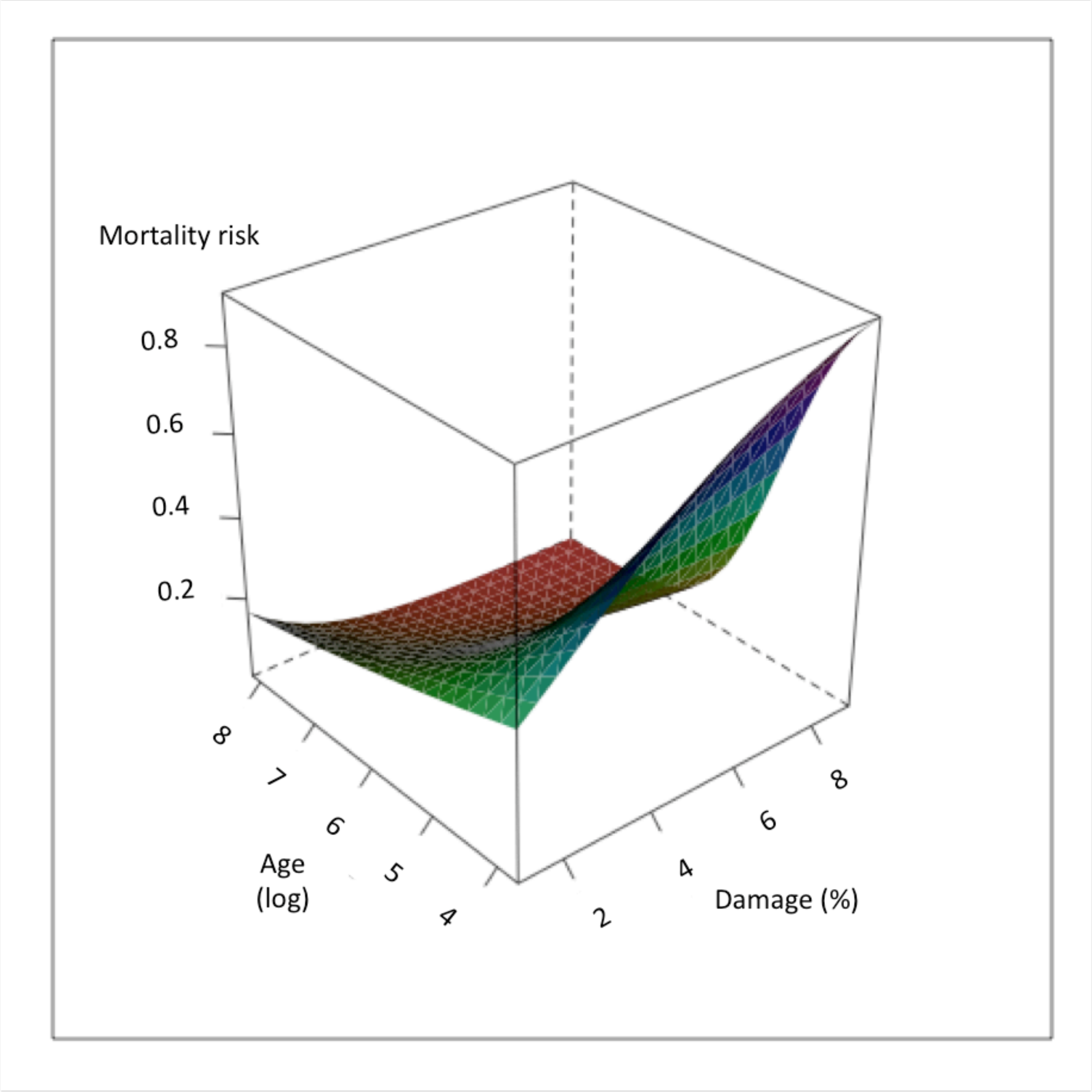


Figure 3.1. Probability of mortality as a function of the age and the amount of damage of the seedling. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

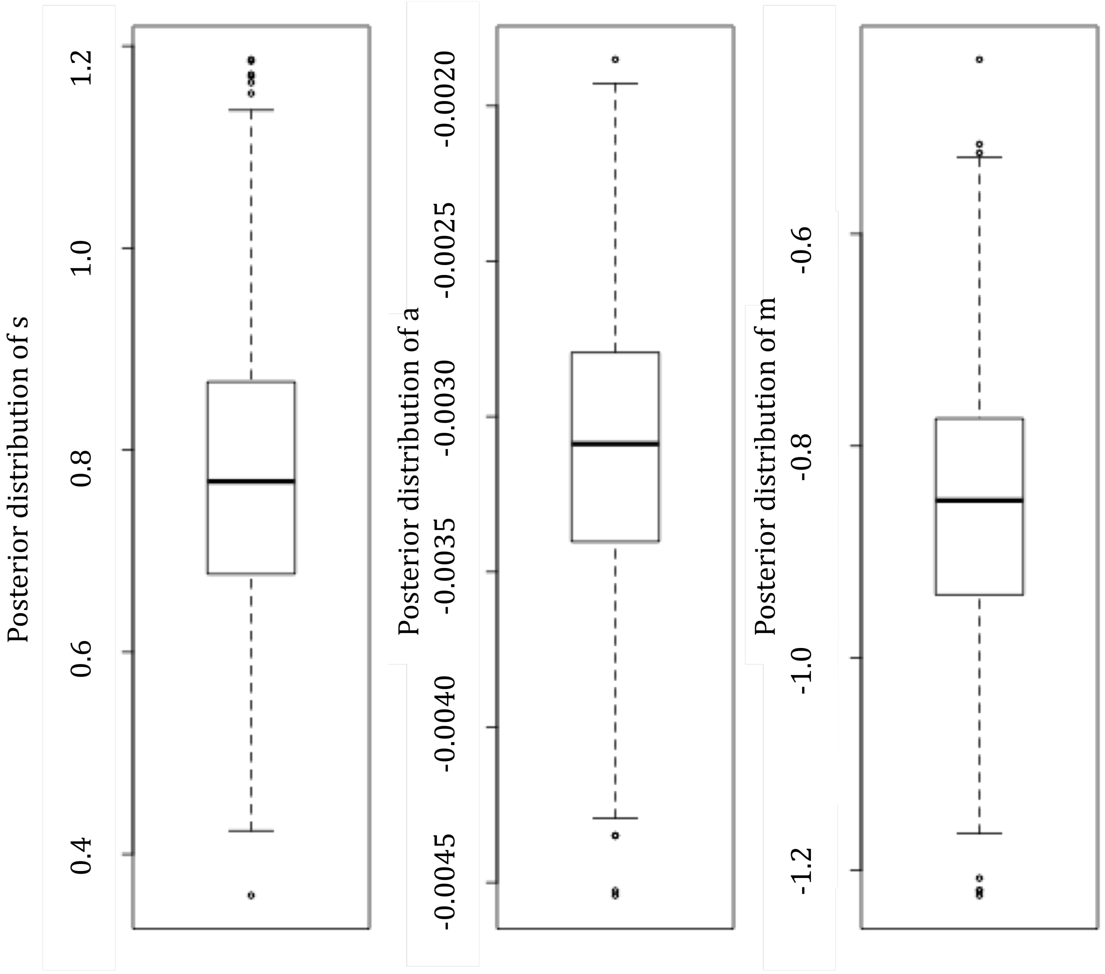


Figure 3.2. Posterior distributions of the effects of damage (s), age (a) on seedling mortality including a mean mortality (m). The wiskers expand to the credible intervals.

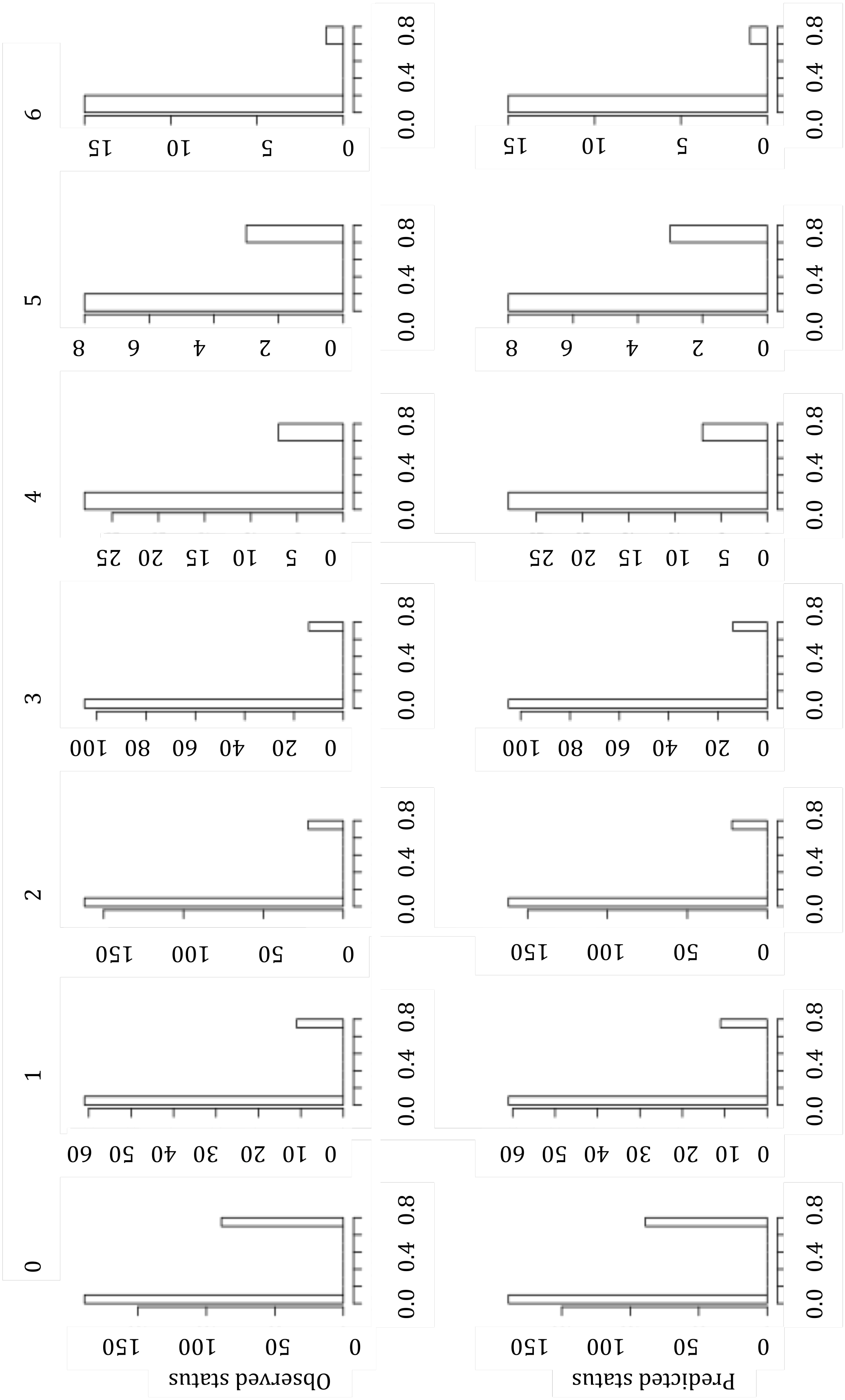


Figure 3.3. Fit of the damage/mortality model (Model 2) across damage category.

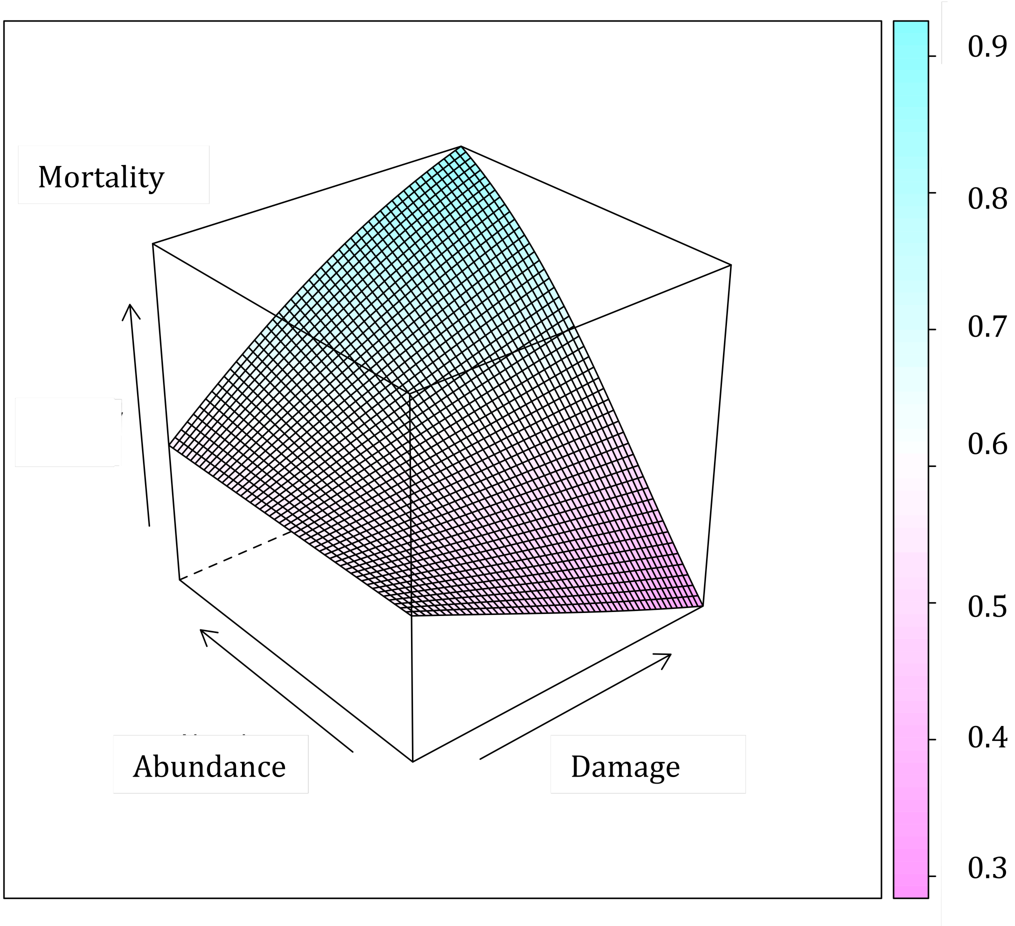


Figure 3.4. Community compensatory trend evidence: increase in mortality risk as species abundance and damage increase. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

LITERATURE CITED

LITERATURE CITED

Bachelot, M. P. E., and R. K. Kobe, 201_. Do seedlings of common tropical tree species host more natural enemy species than seedlings of rare neotropical tree species? A new interpretation of the Janzen-Connell hypothesis. In prep

Beck, S. D., 1965. Resistance of plants to insects. Annual Review of Entomology 10, 207-232.

Boege, K. and R. J. Marquis, 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends in Ecology and Evolution, 20, 441-448.

Brooks, SP. and A. Gelman 1997. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics, 7, 434-455.

Cobb, N. S. and T. G. Whitham 1993. Herbivore deme formation on individual trees-a test-case. Oecologia 94, 496-502.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298 312 in P. J. D. Boer and G. R.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non equilibrium state. Science, 199, 1302-1310.

Connell, J. H., J. G. Tracey, L. J. Webb, 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. Ecological Monographs, 54, 141-164.

Del-Val, E. K., and M. J. Crawley, 2005. Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight british grassland species. Journal of Ecoogy, 93, 1005-1016.

Eichhorn, M. P., R. Nilus, S. G. Compton, S. E. Hartley, and D. F. R. P. Burslem 2010. Herbivory of tropical rain forest tree seedlings correlates with future mortality. Ecology, 91, 1092-1101.

Fine, P. V. A., I. Mesones, and P. D. Coley 2004. Herbivores promote habitat specialization by trees in amazonian forests. Science, 305, 663-665.

Gehring, C. A., N. S. Cobb, et al. 1997. Three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines. American Naturalist, 149, 824-841.

Hulme, P.E. 1994a. Rodent post-dispersal seed predation in grassland: magnitude and sources of variation. Journal of Ecology, 82, 645-652.

Hulme, P.E. 1994b. Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. Journal of Ecology, 82, 873-880.

Hulme, P. E. 1996. Herbivores and the performance of grassland plants: A comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology, 84, 43-51.
Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104, 501-528.

Kobe, R. K. and C. F. Vriesendorp, 2011. . Conspecific density-dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14, 503:510.

Mopper, S., J. B. Mitton, T. G. whitham, N. S. Cobb, and K. M. Christensen 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental-stress. Evolution 45, 989-999.

Parker, I. M. and G. S. Gilbert 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. Ecology 88, 1210-1224.

Silander, J. A., 1978. Density-dependent control of reproductive success in *Cassia biflora*. Biotropica, 10, 292-296.

Zangerl, A. R., J. G. Hamilton, , T. J. Miller, A. R. Crofts, K. Oxborough, M. R. Berenbaum, and E. H. de Lucia 2002. Impact of folivory on photosynthesis is greater than the sum of its holes. Proceedings of the National Academy of Sciences of the United States of America, 99, 1088-1091.

LITERATURE CITED

Bachelot, M. P. E., and R. K. Kobe, 201_. Do seedlings of common tropical tree species host more natural enemy species than seedlings of rare neotropical tree species? A new interpretation of the Janzen-Connell hypothesis. In prep

Beck, S. D., 1965. Resistance of plants to insects. Annual Review of Entomology 10, 207-232.
Boege, K. and R. J. Marquis, 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends in Ecology and Evolution, 20, 441-448.

Brooks, SP. and A. Gelman 1997. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics, 7, 434-455.

Cobb, N. S. and T. G. Whitham 1993. Herbivore deme formation on individual trees-a test-case. Oecologia 94, 496-502.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298 312 in P. J. D. Boer and G. R.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non equilibrium state. Science, 199, 1302-1310.

Connell, J. H., J. G. Tracey, L. J. Webb, 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. Ecological Monographs, 54, 141-164.

Del-Val, E. K., and M. J. Crawley, 2005. Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight british grassland species. Journal of Ecoogy, 93, 1005-1016.

Eichhorn, M. P., R. Nilus, S. G. Compton, S. E. Hartley, and D. F. R. P. Burslem 2010. Herbivory of tropical rain forest tree seedlings correlates with future mortality. Ecology, 91, 1092-1101.

Fine, P. V. A., I. Mesones, and P. D. Coley 2004. Herbivores promote habitat specialization by trees in amazonian forests. Science, 305, 663-665.

Gehring, C. A., N. S. Cobb, et al. 1997. Three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines. American Naturalist, 149, 824-841.

Hulme, P.E. 1994a. Rodent post-dispersal seed predation in grassland: magnitude and sources of variation. Journal of Ecology, 82, 645-652.

Hulme, P.E. 1994b. Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. Journal of Ecology, 82, 873-880.

Hulme, P. E. 1996. Herbivores and the performance of grassland plants: A comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology, 84, 43-51.

Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104, 501-528.

Kobe, R. K. and C. F. Vriesendorp, 2011. . Conspecific density-dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14, 503:510.

Mopper, S., J. B. Mitton, T. G. whitham, N. S. Cobb, and K. M. Christensen 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental-stress. Evolution 45, 989-999.

Parker, I. M. and G. S. Gilbert 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. Ecology 88, 1210-1224.

Silander, J. A., 1978. Density-dependent control of reproductive success in *Cassia biflora*. Biotropica, 10, 292-296.

Zangerl, A. R., J. G. Hamilton, , T. J. Miller, A. R. Crofts, K. Oxborough, M. R. Berenbaum, and E. H. de Lucia 2002. Impact of folivory on photosynthesis is greater than the sum of its holes. Proceedings of the National Academy of Sciences of the United States of America, 99, 1088-1091.

CHAPTER IV

Negative density-dependent mortality varies over time offering a rescue process for seedlings of rare species in a wet tropical forest

ABSTRACT

One of the most widely recognized hypotheses for high alpha tree diversity in the tropics, the Janzen – Connell hypothesis (JC), remains controversial. My previous results indicated that seedlings of common tree species host a higher diversity of aboveground natural enemies than seedlings of rare tree species leading to a higher amount of leaf damage which in turns leads to increasing mortality risk. Therefore, from an aboveground perspective, I found support for the JC and the community compensatory trend (CCT), where common species are at a disadvantage compared to rare species. However, other recent studies have demonstrated that rare versus common species experience more intense negative density dependent mortality, which is the sum of both aboveground and belowground processes. I hypothesized that these contradictory results arise from temporal variation in NDD. Using 10 years of data from La Selva Biological Station (Costa Rica), decomposed into 1 and 5 years time segments, I found that NDD was not constant over time. Although NDD remained stronger for rare species than for common ones in 53 % of the tested time periods, rare and common species suffer equally from conspecific in 41 % of the tested time periods, and rare species were at an advantage compared to common species in 6 % of the tested time periods. Temporal variation in NDD may act as a rescuing process for rare species.

INTRODUCTION

The Janzen – Connell model (JC) hypothesizes that natural enemies of seeds and seedlings are responsible for the maintenance of high alpha tree diversity in tropical forests (Janzen 1970, Connell 1971) via negative density dependence (NDD). I previously tested and brought support to the hypothesis that seedlings of common species hosted a higher diversity of foliar natural enemies than seedlings of rare species (Bachelot and Kobe 201_). Furthermore, I showed that higher diversity of foliar natural enemies was positively correlated with a higher amount of foliar damage which in turn lead to increasing mortality risk in young seedlings (Bachelot and Kobe 201_, Bachelot and Kobe 201_). From an aboveground point of view, my results support the JC and a CCT (Connell 1978, 1984), where common species are at a disadvantage compared to rare species.

A traditional way of assessing the JC is to look at the effect of conspecific neighbors on seedling survival without separating aboveground from belowground enemies. Indeed, at the individual level, a direct prediction of the JC is that at high conspecific seedling density, per-capita survival should be diminished. This effect is known as negative density-dependent mortality. Most studies testing the JC have focused on this mortality pattern (see review by Clark and Clark 1984), with some studies supporting NDD at the individual level (Augspurger 1983a, 1983b, Clark and Clark 1984) and others not (Silander 1978, Boucher 1981). Similarly, at the species level, some studies are consistent with a CCT via NDD (Connell 1984, Webb and Peart 1999, within shade tolerant species Comita and Hubbell 2009), while others are opposed (Klinomoros 2002, Mangan et al. 2010a, Comita et al. 2010).

Net NDD results from the sum of positive and negative below- and above-ground interactions. Belowground, root/mycorrhizae interactions lead to positive feedbacks (Hoshizaki et al. 1997, Bever 2002, Klironomos 2002, Castelli and Gasper 2003, Mangan et al. 2010b), whereas soil pathogens and soil chemicals generally produce negative feedbacks (McCarthy-Neumann and Kobe 2008). Moreover, there is growing evidence in the literature that aboveground trophic interactions (between the host seedling and aboveground natural enemies) influence belowground biotic interactions (Hooper et al. 2000, Van der Putten et al. 2001, Wardle 2002; Wardle et al. 2004, Bardgett 2005, Bardgett and Wardle 2010).

Previous studies linked NDD and species abundance (Klironomos 2002, Mangan et al. 2010a, Comita et al. 2010). However, these studies were generally short-term, Comita et al. (2010) used only five years of data (for individuals > 20 cm height). This could be problematic because rare species at the time of the study will not necessarily remain rare in future years. Studying biological mechanisms within a temporal framework is important (e.g. Ewel and Hiremath 2005, Bardgette et al. 2005) because interactions between soil organisms and roots can change over short time scales (seasons). Plant influences on nutrient availability also can operate over successional time scales lasting thousands of years (Bardgett et al. 2005, Miki et al. 2010). Thus, it is important to examine variability in the strength and direction of NDD over time.

For this study, my main objective was to examine seedling mortality as a function of local conspecific density (i.e., negative density dependence, NDD), which includes both above- and belowground effects (ANDD and BNDD). A further goal was to assess if species susceptibility to NDD was related to the species abundance at the community level. I expect to find 1) variation of the effect size of this conspecific influence over time and 2) that rare species are periodically favored by NDD compared to common species.

METHODS

Site

This project was conducted at La Selva Biological Station in the Atlantic Lowlands of Costa Rica (10º 26’N, 84º 00’ W). The core data set consists of five 1 x 200-m belt transects which were established across a soil gradient representative of the landscape-level occurrence of major soils: three transects on residual soils, one on older alluvial soils, and one on recent alluvial soils. All newly germinating and surviving woody seedlings were systematically surveyed in 1000 1-m^2 plots every six weeks since 2000 (Kobe and Vriesendorp 2009). Liana and small palm seedlings were excluded from this study because adults were not mapped. All trees (> 5 cm diameter) within 20 m of the seedling quadrats were mapped and identified.

Survival time

Based on 10 years of data, I evaluated survival status for each seedling for seven different time intervals: ten intervals of one years and two intervals of five years. These two intervals were selected in order to 1) assess the time period of NDD variations, and 2) make direct comparisons with Comita et al. (2010), which reflect a 5-year data set.

Conspecific density and species abundance

I calculated the average conspecific density occurring in the same quadrats experienced by a seedling over its lifetime. At the community level, abundance was defined as the sum of the basal areas of conspecific adult trees present along the five transects in order to avoid correlation between species abundance and conspecific seedling density. Note, that in the second chapter, species abundance was defined as the seedling abundance over the past five years that is significantly positively related to sum of basal tree area (Figure C.1).

Statistical analyses

To test temporal variation of NDD and how species abundance influences NDD, I use a Bayesian model of seedling survival for each modeled time interval. Following Comita et al. (2010), I combined an individual level and a community level analyzes in a Bayesian framework as following:

$$
\begin{aligned}
&s_{i,j} \sim dbern(p_{i,j}) \\
&P_{i,j} = \mathrm{log}\,it^{-1}(\mu + NDD_j / \mathrm{max}_j * conspecific_i) && \text{(Model 1)} \\
&NDD_j = mean + a * \mathrm{log}(1\_abundance_j)
\end{aligned}
$$

Where s_{ij} stands for the status of the seedling i of species j at the end of the time interval: 0 indicates an individual’s death; 1 indicates its survival. Hence, p_{ij} represents the probability of surviving. To correct for differing potential numbers of conspecific neighbors across species I used max_j that represents the potential neighbor density of the species j (Kobe and Bachelot unpublished). I used a non-informative proper prior for each of the parameters (dnorm (0,100))

In accordance with Comita et al. (2010), I considered mean probability of survival to be independent of community factors, whereas NDD was considered dependent on species mean and species abundance effects. The model was run using R and JAGS. A total of 34 survival models were fitted using an iterative process called Markov Chain Monte Carlo (MCMC) that sample from posterior distributions defined by prior distributions and likelihood of the data: I ran two MCMC chains for each 1-year interval (2000, 2001, …, 2009), two MCMC chains for each 2-year interval (2000 to 2001, 2002 to 2003, 2004 to 2005, 2006 to 2007, 2008 to 2009), and two MCMC chains for each 5-year interval (2000 to 2004, 2005 to 2009). Convergence at each time interval was assessed using the Gelman criteria (Brooks and Gelman 1997). Significances of *a* and *mean* were determined by non-overlap of posterior distributions with 0.

I also fitted the same model in a hierarchical framework, in which NDD was sampled from a normal distribution whose mean was proportional to species sum of basal area, and I decided to select the non-hierarchical model since the posterior distributions of the two models overlapped and the DIC, calculated using pV (Gelman et al. 2004), favored the non-hierarchical model.

To better understand potential temporal changes in NDD, I also I also fit models for individual species, so that the influence of particular species on temporal dynamics in NDD could be assessed. For each interval of time, species with more than 20 individuals were selected, and the first level of the previous model was fitted using MCMC; for each species, s_i is the status of the seedling *i*, p_i stands for the probability of surviving and is modeled as the inverse logit of a mean survival probability across individual (*mean*) plus the conspecific neighbor effect (NDD). *Conspecific$_i$* stands for the density of conspecific neighbors of the individual *i*.

$$s_i \sim dbern(p_i)$$
$$p_i = \operatorname{logit}^{-1}(mean + NDD * conspecific_i) \qquad \text{(Model 2)}$$

Note that because this model is species specific, I did not correct for differing potential numbers of neighbors across species.

For each model, I used two chains with over-dispersed initial values in order to assess convergence using the Gelman criteria (Brooks and Gelman 1997). Posterior distributions of *NDD* for each interval were recorded. Significance was assessed by non-overlap of the posterior distribution with 0. To test the models, I simulated data from the model and re-estimated the posterior distributions of the parameters using the simulated data. Finally, I assessed the predictive value of the models by predicting 20% of the data using the remaining 80% to fit the model. I repeated this method 5 times by rotating the 20% of data set aside while fitting the model in order to fully predict 100% of the data.

RESULTS

Conspecific neighbor effect (Model 1)

At the 5-year scale, NDD switched from being independent of species community abundance (from 2000 to the end of 2004) to being higher in rare seedlings (from 2005 to the end of 2009) (Table 4.1, Figure 4.1). The mean NDD across species was significantly different from zero in both 5-years intervals (Figure C.2). However, no significant difference between the mean NDD of the first 5-years interval and the second was detected.

At the 1-year intervals, fluctuations in NDD mechanisms were also detected (Table 4.2, Figure 4.2). In 2000, 2004, 2005, and 2008, NDD was not related to species abundance. During 5 of the other years (2001, 2002, 2003, 2006 and 2007), seedlings of rare species were more affected by NDD than seedlings of common species. In 2009, a significant change in the direction of the effect of species abundance on NDD occurred; rare species suffered less NDD than common species. Among the different years for which NDD was negatively correlated with species abundance, only 2002 was significantly higher than 2006. The mean NDD across species also showed fluctuations from year to year (Table 4.2, Figure C.3); in 2000, 2004, and 2007 the mean NDD across species was not significantly different from zero. In 2001, 2002, 2003, 2005, 2006, and 2008, mean NDD across species was different from zero but similar to each other with the exception of 2003 mean NDD and 2008 mean NDD. In 2009 there was a significant decrease of the mean NDD experienced by the species on average. This corresponds to the year during which rare species were suffering less NDD than common species. Taken together, the results showed a positive impact of conspecific neighbors for each species in 2009 (Figure 4.3). This conspecific advantage was stronger for rare species than for common species.

Species-specific NDD (Model 2)

At the species-specific level, only 14% of the models showed a significant density-dependent effect (Table 4.3, Figure 4.4), with 10 significant posterior distributions out of 73. Among these significant density dependence effects, three were negative, indicating a positive effect of conspecifics of *Hernandia didymantha* and *Pentaclethra macroloba* over the 2006 to 2007 and 2008 to 2009 intervals, and of *Anaxagorea crassipetala* over the 2008 to 2009 interval. I did not have enough data to test for significant change in NDD at the species level. However, interestingly, the negative effects of conspecifics of *Coussarea hondensis* (a common species) tended to significantly increase over time (Table 4.3).

I verified the validity of the results by testing for temporal dependence in all the residuals across time period models. The lack of temporal variation in the residuals confirmed that the results are not an artifact of the model used.

DISCUSSION

Summary

Considering the net effect of all density-dependent processes, rare species were subjected to more intense negative density dependence than common species 51% of the time. A related study (Bachelot and Kobe 201_) that focused on foliar damage documented the opposite pattern, that foliar damage and mortality risk via damage (Bachelot and Kobe 201_) increased with species community abundance. Thus processes other than density-dependent leaf damage (e.g., soil-borne agents) must have been operating very strongly to counteract this trend and generally lead to a dominant pattern where rare species experience stronger NDD. Nevertheless, the direction and strength of the relationship between local NDD and a species community abundance varied over time acting as a rescuing process for rare species 6% of the time.

NDD often disadvantages rare species compared to common species

The result of my analysis of changes in NDD over time is more often consistent with a rare species disadvantage (Klironomos 2002, Mangan et al. 2010b, Comita et al. 2010). After correcting for differing scales of conspecific neighbor densities, common species demonstrated a lower NDD than rare species in 53% of the analyses (9 time intervals out of 17). These results and previous studies (Klimonoros 2002, Mangan et al. 2010b, Comita et al. 2010) cast doubt upon a general CCT, especially when considered at the whole seedling level. As highlighted in the introduction NDD is the sum of both above- and belowground mechanisms. Given that an earlier related study found that leaf damage increased with species community abundance, the opposite direction of conspecific neighbor effects on whole seedling mortality implies a dominance of belowground NDD (BNDD). Consistent with these results, Mangan et al. (2010a) found a restricted contribution of aboveground foliar enemies on NDD, and Hoshizaki et al. (1997) found NDD patterns even without aboveground herbivory. Therefore, future studies should separate ANDD and BNDD and examine the balance between the two processes as linkages between aboveground and belowground (Bardgett and Wardle 2010).

NDD changes over time

I found that rare species occasionally (6% of the time) suffer from lower NDD than common species, which could act as a “rescuing process,” allowing some seedlings of rare species to eventually recruit to the sapling stage during a “good NDD year” (such as in 2009). This rescuing process is not ubiquitous (1 time interval out of 17), however 41% of the analyses revealed that rare and common species were suffering from similar NDD. These results are consistent with my hypotheses that rare species would often be disadvantaged compared to common species due to NDD, and that NDD has temporal variation (hypotheses 4 and 5). However, the conspecific neighbor effect is not always consistent with the Janzen-Connell hypothesis since conspecific neighbors favor some species during some year intervals via positive feedbacks (for example the 2-year interval 2006-2007). Evidence for positive feedbacks has been found by multiple studies and it may be one reason why JC is controversial (see Clark and Clark 1984). Environmental temporal heterogeneity could be responsible for variation in NDD since some micro-environment are favorable for survivor such as high light gaps at the local scale. However, I used data from 5 transects so unless good micro-environment appeared across the landscape in 2009, my results are not likely to mirror the effect micro-environment.

Temporal variation in NDD was detected over a period of 10 years, suggesting that level of NDD is not inherent to the tree species. If NDD were inherent to the species, the change would be expected to occur over tree generations. The specific agents responsible for NDD are still unknown, but could include chemical elements (McCarthy-Neumann and Kobe 2010), pathogens (Mangan 2010b), and mycorrhizae (Bever 1997, 2003, Bonanomi et al. 2005, Kardol et al. 2007, Van der Heijden 2008, Kulmatiski et al. 2008). A rapid change in NDD could arise from changes in pathogens and mycorrhizae due to their fast generation times (Wu and Li 1985, Li et al. 1987).

NDD variation also could arise from change in soil community composition. There is evidence that arbuscular miccorhizal fungi (AMF) composition changes along with plant composition leading to differing plant-soil feedbacks (zhang et al. 2010, Mangan et al. 2010a). More specifically, Zhang et al. (2010) found that an invasive plant species, equivalent in my model to a rare species becoming common, was able to alter the AMF community to its advantage and that this modification would lead to a decrease of the dominance of native species. If Mangan et al. (2010a) found positive NDD by AMF at the seedling stage of *Apeiba aspera*, Kiers et al. described negative NDD via AMF at the adult stage of *Apeiba aspera* suggesting modification in NDD effect along plant life history due to modification of AMF population in the same direction as Bever (2003) showed. Taken together, these two previous studies stress how soil community can quickly respond to change in plant population leading to modification in NDD.

Variation in effects of conspecific neighbors could equally result from climate effects on host plants (Murphy 1968, Boyce and Daley 1980), and soil organisms (Fenner et al. 2007, Bardgett et al 2008, Bardgett and Wardle 2010). With 10 years of data, I did not find significant associations between NDD versus maximal temperature and rainfall (Figure C.4). However, the two years experiencing a "better NDD" for rare species (2004 and 2009) also experienced the highest maximum rainfall and temperature, which may have promoted increased microbial activity or decreased resistance among seedlings of common species. .

Finally, a decrease in defenses during mast fruiting events (the mast depression hypothesis) (Selas 1997) also could lead to cyclical patterns in NDD; however, I do not have the data to test this idea. . However, I found no significant variation in seedling species composition across time periods (Table C.1, Table C.2, and Table C.3).

Balance between below- and aboveground NDD

Taking together my results indicate that ANDD (aboveground NDD) acts in favor of rare species (Bachelot and Kobe, 201_) whereas BNDD (belowground NDD) often advantages common species; common seedlings host a high aboveground natural enemy richness that leads to high leaf damage which in turns increases the risk of mortality. But, NDD, the sum of ANDD and BNDD, is more often stronger in rare species than common species suggesting that BNDD is strongly advantaging common species (Hoshizaki et al. 1997, Mangan et al. 2010a). The variation of the balance between ANDD and BNDD may be a key mechanism to understand variation in total NDD effects over time and the maintenance of high tree diversity in the tropics. Over the last two decades, the importance of interactions between above- and belowground communities has been widely acknowledged (Hooper et al 2000, Van der Putten et al. 2001, Wardle et al. 2004, Bardgett et al. 2008, Van der Putten et al. 2009, Bardgett and Wardle 2010) along with their importance in plant community structure (Van der Putten 2003, 2009, Van der Heijden et al. 2008, Van der Heidjden and Horton 2009). Theories pertaining to the interactions between above- and belowground communities have been proposed (Masters et al. 1993, Wardle 2002, Bezemer and Van Dam 2005), yet nobody offered a temporal model of species coexistence combining the effect of below- and aboveground processes. My next chapter will fill this gap (Bachelot and Kobe 201_).

Common species tends to show an individual increase in NDD

For more common species, NDD tended to increase over time, especially for *Coussarea hondensis*. I acknowledge, however, that the quantity of data is not sufficient to rigorously test variation of NDD at the species level. However, the most common species *Pentaclethra macroloba* did not experienced an increase in NDD but showed a positive density-dependent effect during 4 out of 10 years, which may relate to the dominance of the species at La Selva. The relative dominance of *P. macroloba* has been attributed to its high tolerance to infertile soils (Hartshorn 1972), and may also reflect a high tolerance to soil pathogens and a high level of mutualistic association with AMF. Positive negative density-dependent mortality could also arise as an artifact of other environmental conditions: more individual seedlings can occur where environment conditions are good and experience higher survivorship. For example, higher irradiance can result in both higher survivorship (Kobe and Vriesendrop 2011) and higher seedling densities. However, *P.*

macroloba and *H. dinanthia* are very common along each transects. Thus, the positive result is not likely the result of an artifact.

CONCLUSION

Consistent with my hypotheses, NDD was often stronger for rare species but is not constant over time. This finding adds a new temporal dimension to the well-acknowledged NDD phenomenon which showed potential to act as a rescuing process for rare species. However, in order to gain a more comprehensive understanding of NDD, future studies should attempt to identify the agents responsible and find the mechanisms behind NDD temporal variation.

Along with my previous study (Bachelot and Kobe 201_), this result reinforces the difference between belowground and aboveground processes. When solely looking at aboveground enemies, my results found an advantage at being a rare species, whereas from the point of view of a total NDD, common species are at an advantage. Taking together my results reinforce the importance of examining ANDD and BNDD over time to understand plant community structure since opposite directions between ANDD and NDD suggest that BNDD may strongly advantage common species.

Table 4.1. Posterior distributions of the different parameters of the survival model at 5-year scale: a is the effect of tree abundance on NDD, m represents the mean NDD effect across species and m2 represents the mean of the survival probability across individuals.

	2000-2004	**2005-2009**
A	0.244 (0.192)	0.319 (0.139)
m	-0.908 (0.893)	-1.066 (0.695)
m2	-4.874 (0.145)	-4.663 (0.146)
p-value	0.495	0.620

Table 4.2. Posterior distributions of the different parameters of the survival model at 1-year scale: a is the effect of tree abundance on NDD, m represents the mean NDD effect across species and m2 represents the mean of the survival probability across individuals.

Intervals	a	m	m2	p-value
2000	0.195 (0.153)	-0.722 (0.685)	-3.537 (0.170)	0.50
2001	0.609 (0.151)	-3.333 (0.902)	-3.263 (0.199)	0.50
2002	0.297 (0.136)	-2.106 (0.774)	-2.386 (0.172)	0.51
2003	0.577 (0.174)	-3.910 (1.034)	-3.284 (0.195)	0.5
2004	-0.063 (0.150)	-0.222 (0.698)	-3.181 (0.170)	0.5
2005	0.0127 (0.243)	-1.587 (1.151)	-3.542 (0.243)	0.48
2006	0.640 (0.094)	-2.390 (0.542)	-3.441 (0.159)	0.54
2007	0.469 (0.134)	-0.914 (0.761)	-4.472 (0.252)	0.5
2008	0.159 (0.114)	-2.691 (0.154)	-0.998 (0.597)	0.47
2009	-0.146 (0.095)	-2.842 (0.189)	1.253 (0.480)	0.53

Table 4.3. Species specific density dependence. mean value of the posterior of of NDD with the standard deviation in parenthesis.

Species	**2000-2001**	**2002-2003**	**2004-2005**	**2006-2007**	**2008-2009**
Apeiba membracea	-82.96 (64.33)		-86.33 (60.96)	-86.82 (64.28)	-90.8 (62.81)
Ardisia fimbrillifera	-1.07 (0.78)	-52.13 (39.02)		-83.05 (64.71)	-54.93 (38.8)
Ardisia nigropunctata	-76.52 (67.44)	-88.13 (62.9)			
Axagorea crassipetala	-84.8 (65.57)		**-0.3 (0.16)**	-89.61 (62.7)	**+0.5 (0.14)**
Borojoa pamensis				-85.13 (62.59)	-85.88 (64.49)
Brosimum lactescens			-53.61 (42.87)		
Capparis pittieri		-0.66 (0.53)	-88.74 (61.67)	-78.82 (69.23)	-87.8 (64.66)
Cassipourea elliptica	-73.61 (75.31)	-87.66 (65.49)	-86.85 (63.37)	-82.12 (67.88)	
Castilla elastica	-84.83 (65.52)	-86.99 (61.93)	-89.19 (64.01)	-82.91 (63.28)	
Colubri spinosa	**-0.53 (0.15)**	**-0.08 (0.03)**	-93.83 (62.39)	-82.38 (66.88)	-86.17 (60.16)
Cordia alliodora	-89.53 (63.60)	-90.51 (63.41)	-87.45 (64.29)	-89.62 (62.83)	-54.4 (38.92)
Cordia bicolor		-86.2 (63.9)	-82.55 (65.27)	-87.06 (66.79)	
Coussarea hondensis	**-0.12 (0.06)**	0 (0.03)	**-0.35 (0.19)**	-0.75 (0.42)	-42.28 (29.99)
Dendropax arboreus		-80.13 (66.65)		-78.17 (67.89)	
Euterpe precatoria					-73.29 (71.37)
Faramea parvibractea				-87.54 (63.79)	-92.1 (63.84)
Goethalsia meiantha	-83.67 (67.63)	-51.23 (37.88)	-82.43 (67.46)	-82.18 (67.25)	-0.71 (1.28)
Guatteria diospyroides	-59.16 (37.97)	-76.81 (70.36)			
Hampea appendiculata	-4.94 (4.71)	-48.73 (34.91)	-45.04 (36.51)	-57.17 (39.55)	-49.77 (39.42)
Herndia didymantha			-46.01 (33.8)	**+0.38 (0.1)**	**+0.44 (0.15)**
Inga pezizifera		-65.21 (61.49)			
Iriartea deltoidea			-53.9 (43.93)	-64.56 (48.1)	-58.53 (46.82)
Lacmellea pamensis		-87.45 (64.28)	-87.57 (65.56)	-80.06 (69.5)	-77.78 (69.07)

Table 4.3. (cont'd)

Laetia procera	-88.09 (69.45)				
Lozania pittieri					-88.79 (65.06)
Neea elegans	-0.37 (0.32)				
Parathesis trichogyne			-89.12 (62.51)	-88.14 (59.52)	
Pentaclethra macroloba	-0.44 (0.42)	-1.32 (0.75)	-56.06 (44.22)	**+0.51 (0.23)**	**+0.49 (0.14)**
Pholidostachys pulchra				-89.49 (62.28)	-54.45 (40.55)
Pourouma bicolor		-87.48 (64.03)	-85.4 (65.85)	-45.62 (31.49)	-64.93 (50.24)
Pourouma minor	-72.69 (74.59)	-71.85 (72.19)			
Prestoea decurrens	-0.24 (0.91)	-56.85 (42.22)	-57.74 (43.13)	-0.64 (0.88)	-68.26 (48.66)
Protium costaricense	-61.06 (43.656)	-44.17 (33.97)	-78.81 (68.47)		
Protium pamense			-81.15 (66.25)	-77.35 (69.91)	
Psychotria pamensis	-80.7 (67.17)		-85 (62.8)	-79.89 (67.33)	-0.01 (0.12)
Pterocarpus rohrii			+0.07 (0.33)		
Richeria dressleri					-87.54 (60.98)
Rinorea deflexiflora	-63.19 (46.31)	-55.64 (42.62)	+0.01 (0.28)	-1.24 (2.44)	-58.93 (41.52)
Simarouba amara	-82.14 (67.93)	-49.51 (37.83)	-1.5 (1.41)	-0.64 (1.51)	-59.38 (47.83)
Socratea exorrhiza		-60.92 (46.93)	-71.86 (71.99)	-75.66 (69.07)	
Tapirira myriantha			-84.8 (68.19)	-91.18 (62.21)	-89.67 (62.55)
Tetragastris pamensis				-89.39 (62.8)	-84.21 (64.6)
Trophis racemosa				-0.49 (0.84)	
Unonopsis pittieri	-45.02 (34.53)		-42.92 (34.18)		
Virola koschnyi	-59.89 (41.49)	-46.35 (38.43)	-42.32 (30.39)	-46.9 (35.63)	-1.11 (55.91)
Virola sebifera	-10.6 (61.90)		-57.38 (78.19)	-55.82 (81.02)	+7.88 (68.36)
Vitex cooperi	-72.15 (73.62)	-57.11 (47.05)	-85.86 (65.94)		-70 (72.49)
Vochysia ferruginea	-85.16 (63.26)	-79 (69.96)	-83.47 (64.79)	-77.62 (69.22)	

Table 4.3. (cont'd)

Welfia regia	-0.35 (1.01)	-1.6 (1.02)	-72.58 (45.67)	-0.95 (0.74)	-66.62 (49.57)

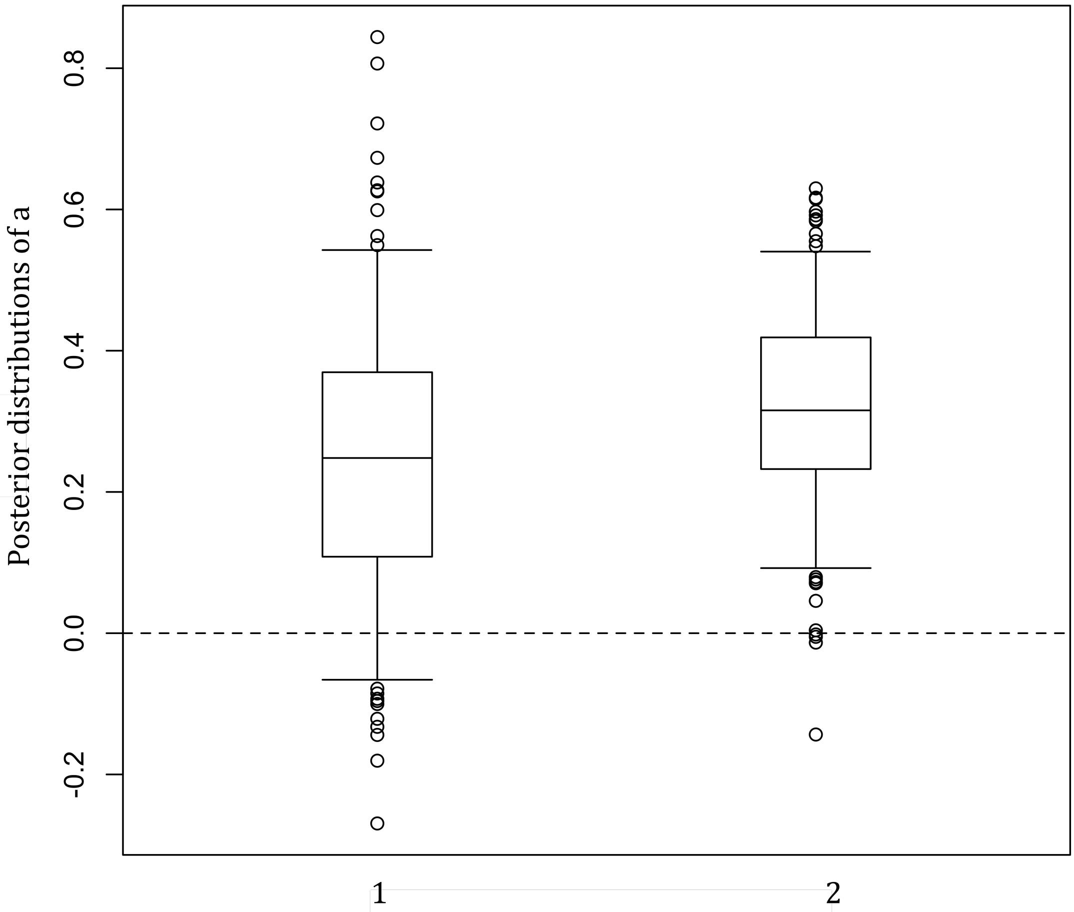


Figure 4.1. Posterior distributions of the effect of species abundance on NDD at each 5-years interval (1: from 2000 to 2004, 2: from 2005 to 2009). The wiskers extend to the credible intervals.

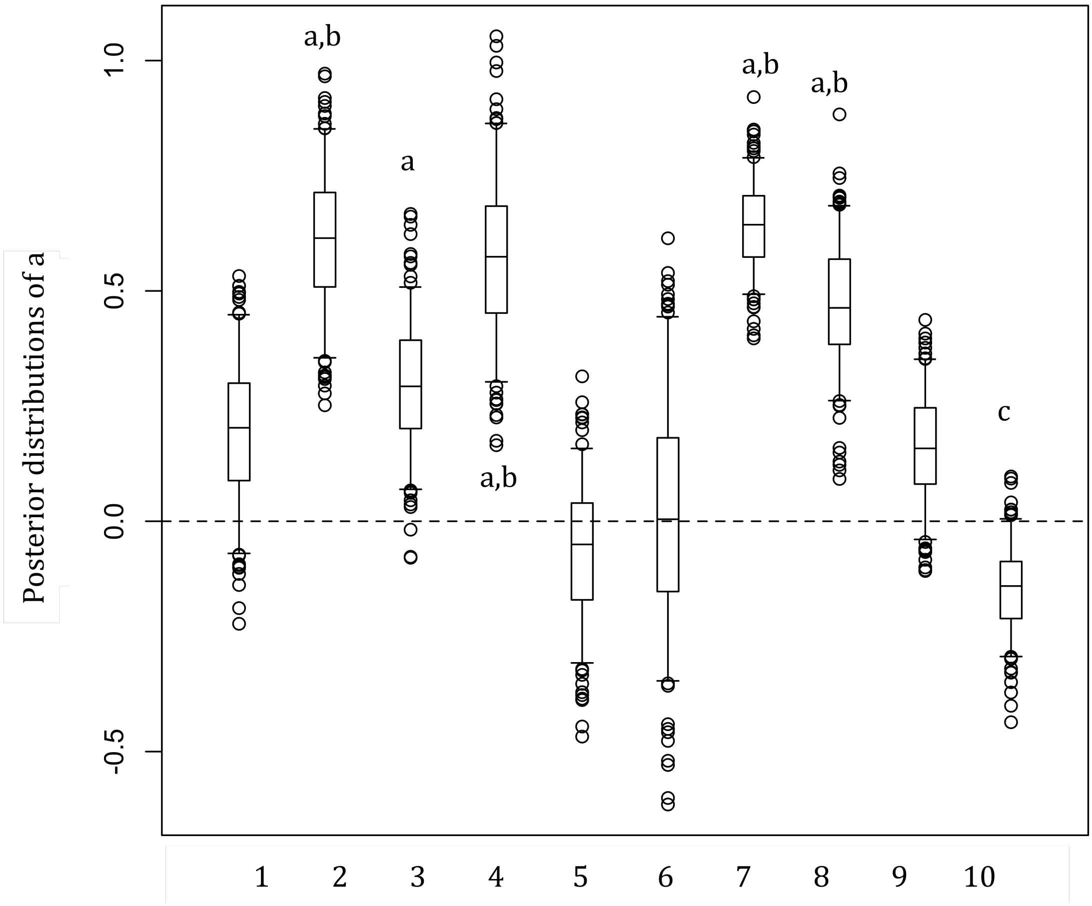


Figure 4.2. Posterior distributions of the effect of species abundance on NDD at each 1-year interval. 1: 2000, 2: 2001, 3: 2002, ..., 10: 2009. The wiskers extand to the 95 credible intervals. Letters show where the distributions are significantly different from each other.

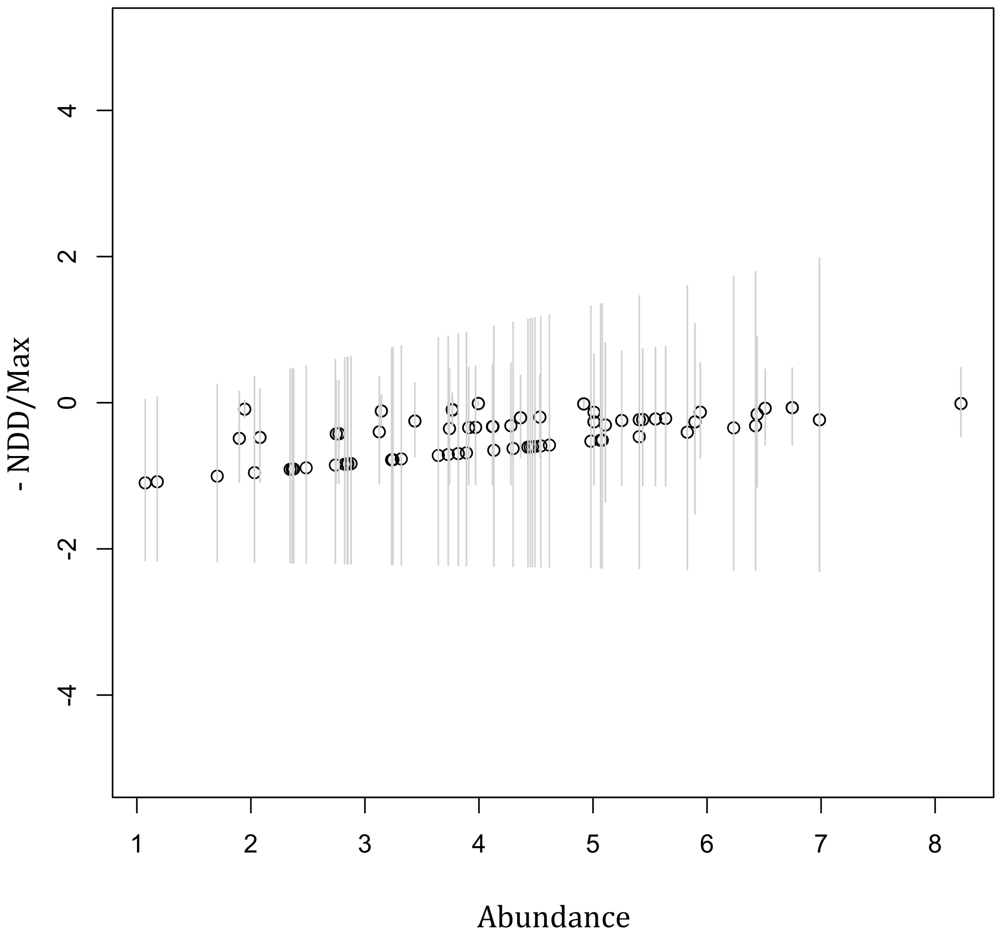


Figure 4.3. Relation between - NDD in 2009, rectified by maximum potential number of conspecific neighbor per species (Max), and abundance of the species. Abundance represents the log transformation of the sum of adult basal area + 1. 2009 is the only year during which rare species are favored compared to common species. Note that each species experience an increase in survival due to conspecific.

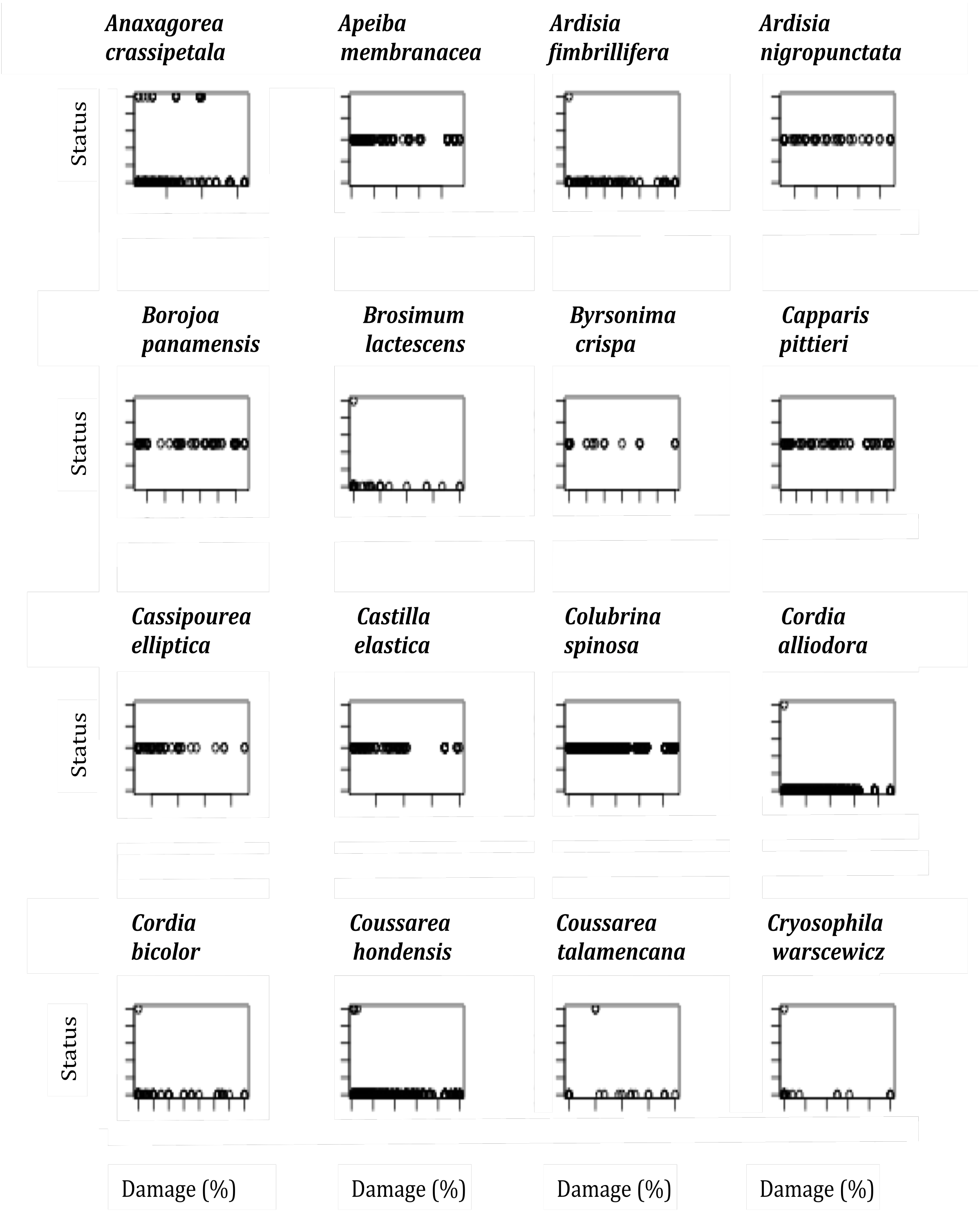


Figure 4.4. Status of the seedlings (0: dead, 1: alive) in function of its damage (%) for each species that was common enough over the 10 years of data (number of seedlings above 20).

Figure 4.4. (cont´d)

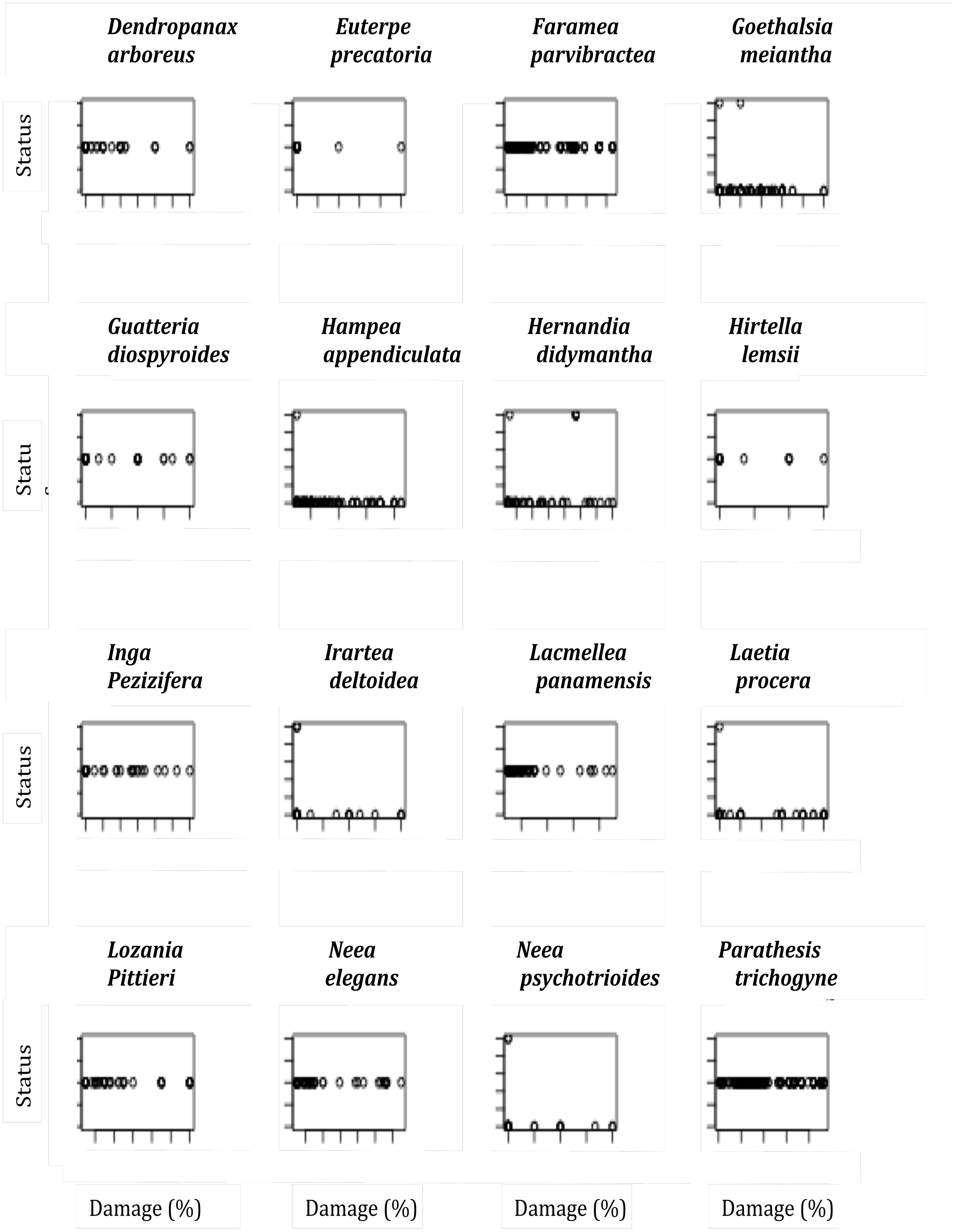


Figure 4.4. (cont'd)

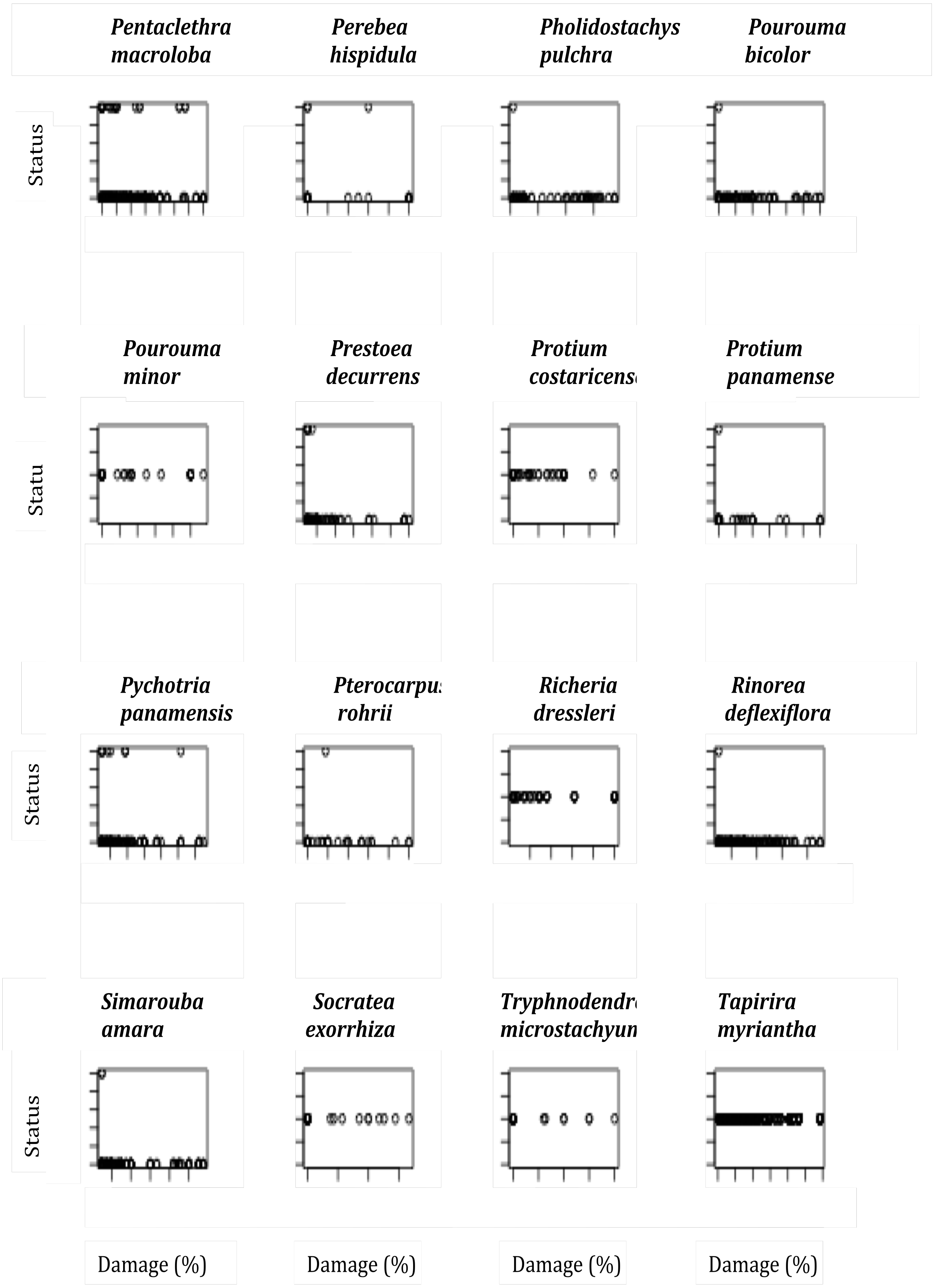
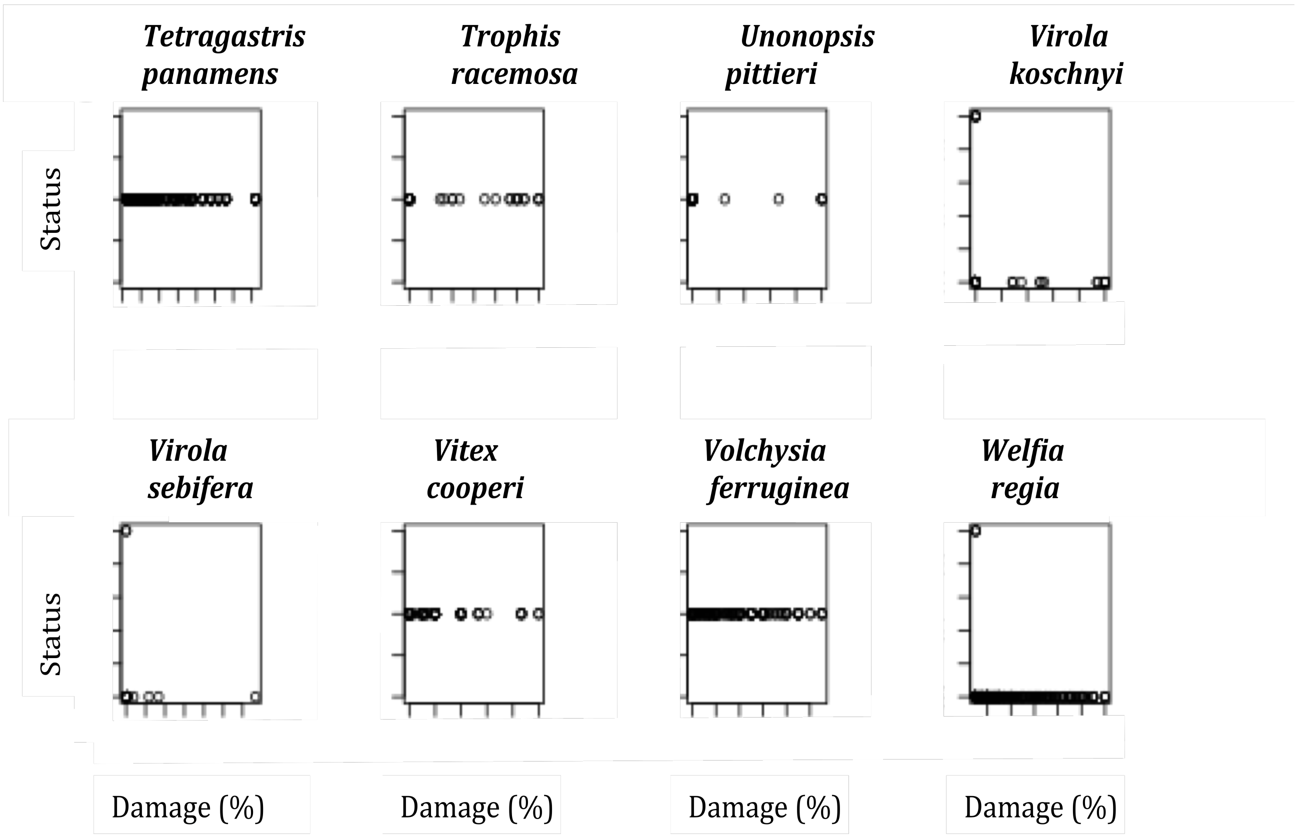


Figure 4.4. (cont'd)



LITERATURE CITED

LITERATURE CITED

Augspurger, C. K. 1983a. Offsping recruitment around tropical trees-Changes in cohort distance with time. Oikos 40, 189-196.

Augspurger, C. K. 1983b. Seed dispersal of the tropical tree, Platypodium elegans, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71, 759-771.

Bachelot, M. P. E., and R. K. Kobe, 201_. Do seedlings of common tropical tree species host more natural enemy species than seedlings of rare neotropical tree species? A new interpretation of the Janzen-Connell hypothesis. In prep

Bachelot, M. P. E., and R. K. Kobe, 201_. Amount of foliar damage predicts future seedling mortality in a wet tropical forest . In prep

Bachelot, M. P. E., and R. K. Kobe, 201_. Tropical seedling abundance cycles; a conceptual model. In prep

Bardgett, R. D., 2005. The biology of soil: a community and ecosystem approach. Oxford University Press, New York.

Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt, 2005. A temporal approach of linking aboveground and belowground ecology. Trends in Ecology and Evolution, 20, 634-641.

Bardgett, R. D., C. Freeman, and R. J. Ostle, 2008. Microbial contributions to climate change trhough carbon-cycles feedbacks. The ISME journal, 2, 805-814.

Bardgett, R. D., and D. A. Wardle, 2010. Aboveground-belowground linkages. Biotic Interactions, Ecosystem processes, and Global change. Oxford series in Ecology and Evolution, Oxford University Press, New York.

Bever, J. D., K. M. Westover, and J. Antonovics, 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85, 561-573.

Bever, J. D., 2002. Host-specificity of AM fungal population growth rates can generate feedback on plant growth. Plant and Soil 244, 281-290.

Bever, J. D., 2003. Soil community feedback and the coexistence of competitors: conceptual framework and empirical tests. New phytologist, 157, 465-473.

Bezemer, T.M., and N. M. Van Dam, 2005. Aboveground–belowground interactions via plant defenses. Trends in Ecology and Evolution, 20, 617-624.

Bonanomi, G., F. Giannino, and S. Mazzoleni, 2005. Negative plant-soil feedback and species coexistence. Oikos 111, 311-321.

Comita, L. S., and S. P. Hubell, 2009. Local neighbors and species' shade tolerance influence survival in diverse seedling bank. Ecology, 90, 328-334.

Comita, L. S., H. C. Muller-Landau, S. Aguillar, and S. P. Hubbell, 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329, 330-332.

Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. A. U. N. Gunatilleke, C. V. S. Gunatilleke, P. Hall,9 K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. LaFrankie, S. Loo de Lao, J. R. Makana, Md. Nur Supardi Noor, A. R. Kassim, S. Russo, R. Sukumar, C.´ n Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa, and T. Zillio, 2006. The importance of demographic niches to tree diversity. Science, 313, 98:101.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298 312 in P. J. D. Boer and G. R.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non equilibrium state. Science, 199, 1302-1310.

Connell, J. H., J. G. Tracey, L. J. Webb, 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. Ecological Monographs, 54, 141-164.

Ewel, J. J., and A. J. Hiremath, 2005. Plant-plant interactions in tropical Forests. In Biotic interactions in the tropics, Their role in the maintenance of species diversity. Cambridge University Press, Cambridge, UK.

Fenner, N., C. Freeman, M. A. Lock, H. Harmens, B. Reynolds, and T. Sparks, 2007. Interactions between elevated CO_2 and warming could amplify DOC exports from peatland catchmetns. Environmental Science and Technology, 41, 3146-3152.

Gelman, A., J. B. Carlin, and D. B. Rubin, 2004. Bayesian data analysis. Chapman and Hall/CRC press, Florida.

Hartshorn, G. S. 1972. The ecological like history and population dynamics of Pentaclethra macroloba, a tropical wet forest dominant and Stryphnodendron excelsum, an occasional associate. Ph. D. dissertation, University of Washington.

Hooper, D.U., D. E. Bignell, V. K. Brown, L. Brussaard, J. M. Dangerfield, D. H. Wall, D. A. Wardle, D. C. Coleman, K. E. Giller, P. Lavelle, W. H. van der Putten, P. C. de Ruiter, J. Rusek, W. L. Silver, J. M. Tiedje, and V. Wlters, 2000. Interactions between above- and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience, 50, 1049–1061.

Hornfeldt, B., f. O. Lfgren, and B. G. Carlson, 1986. Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. Oecologia, 68, 496-502.

Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104, 501-528.

Kardol, P., N. J. Cornips, M. M. L. Van Kempen, J. M. T. Bakx-Schotman, and W. H. Van der Putten, 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs 772, 147-162.

Kelly, D., 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution, 9, 465-470.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417, 67-70.

Kobe, R. K. and C. F. Vriesendorp 2009. Size of sampling unit strongly influences detection of seedling limitation in a wet tropical forest. Ecology Letters 12, 220-228.

Kobe, R. K. and C. F. Vriesendorp, 2011. . Conspecific density-dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14, 503:510.

Kulmatiski, A., K. H. Beard, J. R. Stevens, S. M. Cobbold, 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters 11, 980-992.

Li, W. H., M. Tanimura, and P. M Sharp, 1987. An evaluation of molecular clock hypothesis using mammalian DNA sequences. Journal of Molecular Evolution,25, 330-342.

Mangan, S. A., E. A. Herre, and J. D. Bever 2010a. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant-soil feedback. Ecology 91, 2594-2603.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever 2010b. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466, 752-U710.

Masters, G. J., V. K. Brown, and A. C. Gange, 1993. Plant mediated interactions between above- and below-ground insect herbivores. Oikos, 66, 148-151.

McCarthy-Neumann, S. and R. K. Kobe 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. Ecology, 89, 1883-1892.

Miki, T., M. Ushio, S. Fukui, and M. Kondoh 2010. Functional diversity of microbial decomposers facilitates plant coexistence in a plant-microbe-soil feedback model. Proceedings of the National Academy of Sciences of the United States of America, 107, 14251-14256.

Murphy, P.G. and A. E. Lugo, 1968. Ecology of tropical dry forest. Annual Review of Ecology and Systematics, 17, 67-88.

Nilsson, S. G., 1985. Ecological and evolutionary interactions between reproduction of beech Fagus silvatica and seed eating animals. Oikos, 44, 157-164.

Perala, D. A., A. A. Alm, 1990. Reproductive ecoloof birch. Ecological Management, 32, 1-38.

Selas, V., 1997. Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. Oikos, 80, 257-268.

Silander, J. A., 1978. Density-dependent control of reproductive success in *Cassia biflora*. Biotropica, 10, 292-296.

Silvertown, J. W., and L. J. Doust, 1993. Introduction to plant population biology. Blackwell, Oxford.

Van Breemen N. 1993. Soils as biotic constructs favouring net primary productivity. Geoderma, 57,183-211.

Van der Heijden, M. G. A., S. Verkade, and S. J. De Bruin, 2008. Mycorrhizal fungi reduce the negative effects of nitrogen enrichment on plant community structure in dune grassland. Global Change Biology, 14, 2626-2635.

Van der Heijden, M. G. A., and T. R. Horton, 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. Journal of Ecology, 97, 1139-1159.

Van der Putten, W. H., L. E. M. Vet, J. A. Harvey, and F. L. Wackers, 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends in Ecology & Evolution, 16, 547-554.

Van der Putten, W. H., 2003. Plant defense belowground and spatiotemporal processes in natural vegetation. Ecology, 84, 2269-2280.

Ven der Putten, W. H., 2009. A multitrophic perspective on the functioning and evolution of facilitation in plant communitites. Journal of Ecology, 97, 1131-1138.

Van der Putten, W. H., R. D. Bardgett, P. C. Ruiter, W. H. G. Hol, K. M. Meyer,T. M. Bezemer, M. A. Bradford, S. Christensen,M. B. Eppinga, T. Fukami, L. Hemerik, J. Molofsky, M. Schädler,C. Scherber, S. Y. Strauss, M. Vos, and D. A. Wardle, 2009. Empirical and theoretical challenges in aboveground-belowground ecology. Oecologia 161, 1-4.

Wardle, D. A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton, NJ.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setala, W. H. van der Putten, and D. H. Wall, 2004. Ecological linkages between aboveground and belowground biota. Science, 304, 1629-1633.

Webb, C. O. and D. R. Peart 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology 80, 2006-2017.

Wu, C. I., and W. H. Li, 1985. Evidence for higher rates of nucleotide subsitution in rodent than in man. Proceedings of the National Academy of Sciences of the United States of America, 82, 1741-1745.

Zangerl, A. R., J. G. Hamilton, , T. J. Miller, A. R. Crofts, K. Oxborough, M. R. Berenbaum, and E. H. de Lucia 2002. Impact of folivory on photosynthesis is greater than the sum of its holes. Proceedings of the National Academy of Sciences of the United States of America, 99, 1088-1091.

Zhang, Q., R. Y. Yang, J. Tang, H. Yang, S. Hu, and X. Chen 2010. Positive Feedback between Mycorrhizal Fungi and Plants Influences Plant Invasion Success and Resistance to Invasion. Plos One, 5.

CHAPTER V

Tropical seedling abundance cycles; a conceptual model

ABSTRACT

The maintenance of tropical tree species diversity remains a challenging problem for ecology. Many models have been proposed to explain species coexistence but few have incorporated belowground and aboveground processes within a temporal framework. I propose a conceptual model that tights together aboveground natural enemy diversity with total negative density dependence that is dominated by belowground conspecific effect (BNND). My model successfully predicts coexistence of tree species at the seedling stage via abundance cycles.

INTRODUCTION

This idea of chronic patterns of low and high species abundance is not new; ecologists have been studying population cycles for several decades (Elton 1942, MacArthur 1968, 1970, Travis 1990, Vandermeer 1993, Mueller 1997, Ferriere 1999, 2006, Berryman 2002). Rare species, including animals (Vandermeer 1982, Hanski 1985, Rosenzweig and Molino 1997), pathogens, and crop pests (Anderson and May 1992), are not always rare but follow a pattern of "intermittent rarity" such that they remain rare for a long period of time and their abundance eventually escalates for a brief period. A mathematical analysis of "intermittent rarity" stressed that the period of the cycle is irregular but that the episodes of rarity occurs according to a -3/2 power law, in which the logarithm of the frequencies of rarity episodes is negatively linearly correlated to the logarithm of the time spent in rarity, with a slope of -3/2 (Ferriere and Cazelles 1999). "Intermittent rarity" is not the only abundance cycle that occurs in nature but regular populations also appear due to negative feedback loop between two or more species (Berryman 2002). Six causes of negative feedback loop have been proposed to explain population cycles (Berryman 2002); physical effect, predator effect (Lokta 1925, Volterra 1926), pathogen effect (Anderson and May 1992), plant effect (Elton 1942, Pitelka 1957), maternal effect and genetic effect create oscillations between high and low abundance. Cycles have been observed in mammals (Boutin et al. 2002, Hanski and Henttonen 2002), birds (Hudson et al. 2002), fish (Ferriere 1999, 2006) and insects (Munster-Swendsen 2002, Reeve and Turchin 2002). However, this oscillatory process is sensitive to the other processes governing population demography and can easily become chaotic under the influence of stochastic environmental fluctuation or once adding a suprapredator (Dercole et al. 2010).

Understanding abundance cycles is an important goal in ecology (Krebs 1996). The branch of ecology that attempts to understand high alpha tree diversity in the tropics traditionally follows one of two approaches, ecological or evolutionary, with the former assessing negative density dependence (Lotka 1925, Volterra 1926), resource partitioning (MacArthur 1958), or natural enemies (Janzen 1970, Connell 1971), and the latter integrating pollinators or natural enemies and plant co-evolution (Van Valen 1973). According to the Lotka-Volterra model (LV), an ecological model, under specific conditions, predators and prey can reach a periodic, stable equilibrium (Chen 2006).

Interactions between hosts and natural enemies are expected to evolve under natural selection that includes ecological selection (Fritz and Simms 1992). Plants are the host to both above and belowground natural enemies. Thus, evolutionary and ecological pressure will act upon the interactions between host and both above and belowground enemies. I hypothesize that such processes are occurring between tropical seedlings and their above and belowground enemies. I propose that due to these mechanisms the abundance of a rare species will increase over evolutionary and ecological time. However, in a resource- and space-limited environment, such as a wet tropical forest, it is not possible for up to 300 hundred-tree species (Valencia et al 1994), to coexist in equally common abundances (Hutchinson 1948). Therefore, if evolutionary and/or ecological selection allows a more infrequent species to become more common, the mechanisms must be also acting to reduce the abundance of a more common species. In a tropical forest, this dynamism would result in tree species abundance continually fluctuating over long-term evolutionary time and short-term ecological time (Terborgh at al. 2002, Wills et al. 2006). In this chapter, I would like to propose a conceptual model of seedling abundance dynamics at the ecological scale.

Many aboveground and belowground enemies prey upon seedlings. Below- and aboveground communities are spatially separated but via their direct and indirect action on plants, they interact. Until the last decades, soil ecologists were working in ignorance of aboveground processes, as aboveground ecologists ignored belowground organisms (Wardle 2002). Several studies suggested the importance of studying the interface of below- and aboveground ecology (Vitousek and Walker 1989, Lawton 1994, Jones and Lwaton 1995, Wardle 2002, De Deyn and Van der Putten 2005, Bardgett 2005, Bardgett and Wardle 2010), yet no demographic cycle model has simultaneously incorporated below and aboveground processes. Therefore, one could adapt the LV model to them by separating the prey (seedlings of different tree species) from the aboveground and belowground predators. I previously showed that aboveground natural enemy richness was higher on seedlings of common tree species (Bachelot and Kobe 201_). High diversity of natural enemies is correlated to high amount of aboveground damage that in turns leads to high mortality risk (Bachelot and Kobe 201_). Therefore, aboveground predators preferentially target seedling of common tree species putting seedlings of rare tree species at an advantage, which is consistent with a community compensatory trend (CCT) (Connell 1978, 1984); Natural enemies should preferentially target seedlings of common species, therefore disadvantaging them compared to seedlings of rare tree species. This mechanism could maintain diversity, however conspecific effect has been shown to be more often disadvantaging for rare species (Klimonoros 2002, Comita et al. 2010, Bachelot and Kobe 201_). Under aboveground enemies and conspecific effect, seedlings abundance would change over time. The direction of this change would depend on the relative effect of the two mechanisms. I believe that the variability of NDD over time (Bachelot and Kobe 201_) along with several ecological mechanisms could lead to seedling species abundance cycles that in turn would favor species coexistence in the tropics.

Here, I aim to offer a new conceptual model that unifies aboveground natural enemies with NDD dominated by belowground conspecific effect (BNDD) in order to better describe demographic trajectories of tropical tree species. After a brief description of this ecological model, I will show how a species can progress from rarity to commonness due to the ecological advantage of hosting few aboveground natural enemy species and to decreasing BNDD. I also will discuss the opposite path, whereby a common species regresses to rarity because of high natural enemy richness and increasing BNDD. Accordingly, I will evaluate the mathematical feasibility of such a conceptual model.

GENERAL DESCRIPTION OF THE MODEL

For this model I am making a distinction between the aboveground-natural enemies and the agents of NDD. Aboveground natural enemies may act as agents of NDD however, previous studies did not find significant increase of aboveground natural enemies with increasing conspecific neighbor density (Hoshizaki et al. 2009, Bachelot and Kobe 201_). For the purpose of my conceptual model I consider the belowground part of NDD thatis an intra-specific mechanism leading to higher mortality at high conspecific seedling density (BNDD). Several studies have assessed NDD across species (Augspurger 1983a, b, 1984, Clark and Clark 1984, Schupp 1988, 1992, Howe 1990, Hammond and Brown 1998, Webb and Peart 1999, Parker and Clay 2000, Gilbert et al. 2001, Peters 2003, McCarthy-Neumann and Kobe 2008); however, few have tested whether soil pathogens, soil chemicals, mycorrhizae, or aboveground natural enemies were the agents responsible for NDD (Bever

2002, Klironomos 2002, Castelli and Gasper 2003, McCarthy-Neumann and Kobe 2008, Mangan et al. 2010b). Most existing evidence suggests that NDD is largely caused by belowground agents (Augspurger 1984, Ehrenfeld et al. 2005, McCarthy-Neumann and Kobe 2008, Hoshizaki et al. 2009, Mangan et al. 2010a). Therefore, for my model, I should separate the two types of agents responsible for NDD; aboveground enemies responsible for aboveground damage leading to mortality (ANDD agents) and belowground enemies (BNDD agents).

My model proposes that under the pressure of the two dependent forces, BNDD and aboveground natural enemy richness, tropical tree species abundance fluctuates over ecological time (Figure 5.1). Thus, at any given time, the tropical tree community will contain both common and rare species. A rare species experiences both high BNDD and low aboveground natural enemy richness (Comita et al. 2010, Bachelot and Kobe 201_). These two forces are, a priori, opposing and act on tree species abundance over ecological time. Despite at first of a high mortality due to BNDD, I will show how seedlings of rare tree species increase their relative abundance (part A and B in Figure 5.1). Conversely, a common species experiences high aboveground natural enemy richness leading to a high mortality (Bachelot and Kobe 201_). Low BNDD may be expected to preserve the abundance of common species; however, I will show how a high diversity of aboveground natural enemies leads to higher mortality, eventually causing more common species to become less common (Part C and D of Figure 5.1).

It is important to note, that when a species suffers from low BNDD, it hosts a high diversity of aboveground natural enemies and vice versa. This assumption is empirically supported; Comita et al. (2010) found that common species suffer from low NDD. Above ground NDD (ANDD) is consistent with the CCT while NDD shows opposite patterns to CCT

(Bachelot and Kobe 201_), therefore BNDD must be very strong. This is consistent with previous findings that NDD is driven by belowground agents (Augspurger 1984, Ehrenfeld et al. 2005, McCarthy-Neumann and Kobe 2008, Hoshizaki et al. 2009, Mangan et al. 2010a). Evidence of opposing effects of ANDD and BNDD on plant community structure was also shown (Brown and Gange 1989); the authors found that aboveground insecticides decrease plant species richness whereas belowground insecticides promote plant species richness. In addition, recent finding found that common species also hosts a high diversity of aboveground natural enemies (Bachelot and Kobe, 201_). Therefore, a species with high aboveground natural enemies has a low BNDD and vice versa. Until recently, the link between belowground and aboveground communities affecting plants was ignored (Bardgett and Wardle 2010). Interactions between belowground and aboveground are complex and likely to be species-specific (Wardle 2002), but evidence suggests that aboveground and belowground have opposite effect on plant tissue growth (Masters et al. 1993) In a conceptual model developed by Masters et al., aboveground herbivores are thought to negatively impact belowground herbivores via decreasing root tissue growth, whereas belowground herbivores would promote aboveground plant tissue production via stress responses. Therefore, a seedling host would not suffer at the same time from both high (respectively low) aboveground and belowground enemies.

In my proposed model, hosted aboveground natural enemy richness, represented by the left y-axis, is strongly positively correlated with plant species abundance over five-years time scale. The model assumes aboveground natural enemy richness impacts seedling survivorship. This assumption was tested in a previous study during which I found that increasing aboveground natural enemy richness is positively correlated to increasing aboveground damage that leads to increasing mortality in young seedlings (Bachelot and Kobe 201_).

BNDD effect, represented by the x-axis, is inspired by Comita et al. (2010)'s finding that NDD is higher for rare species. However, it is important to note that I am making a different interpretation of their results. Here, my model uses solely BNDD and it assumes that BNDD is inherent to the species but changes over ecological time. Using 10 years of data, I previously showed that NDD was variable (Bachelot and Kobe 201_). Because NDD is thought to be more strongly influenced by belowground agents than aboveground agents (Hoshizaki et al. 2009, Mangan et al. 2010, Bachelot and Kobe 201_), I generalize my findings to BNDD.

Species commonness, represented by the right y-axis, characterizes the demography of the species as the two forces (aboveground natural enemy richness and BNDD) act upon it. The time scale, under which the model is working, is represented by the arrows and their size. The size of the arrow represents the speed of the process to move from one stage of abundance to another. Here, time is the ecological period required for rare/common tree species to experience lower/higher BNDD and aboveground natural enemy populations to respond to changes in tree species abundances. Based on my previous findings, I expect those oscillations to occur at a short time scale (10 to 15 years); aboveground natural enemy richness is sensitive to seedling abundance over the past 5 years (Bachelot and Kobe 201_), and variation of NDD are observed at the 1-year, 2-year and 5-year scales (Bachelot and Kobe 201_).

From rarity to commonness, part A and B in Figure 5.1

Subsequent decrease of initially high BNDD

Even if a rare species gains a relative advantage over common species by hosting a low aboveground natural enemy richness, high BNDD can prevent it from becoming more common and may eventually even bring the species to extinction. Regardless of the agents responsible, BNDD is more likely to be an inherent characteristic of the species and reflects its ability to defend itself against threats. BNDD should thus be strongly correlated with the types of defenses a species has evolved against its belowground natural enemies.

Over ecological time, if BNDD agents, other than chemicals, behave as aboveground natural enemies, they should shift their behavior to target more common species. If BNDD agents are primarily chemicals, Stinson et al. (2006) showed that invading species could reduce the fitness of dominant native species by secreting anti-fungal that alter mutualistic associations between fungi and native species. If a rare species acts as an invading species, then you may expect the rare species to secrete more anti-fungi that would lead common species to lose mutualistic associations (BNDD increase) and rare species to gain mutualistic associations (BNDD decrease). In both cases, BNDD for rare species would be expected to decrease.

My model can thus be viewed as a classical multi-species Lotka-Volterra model, where each population of seedling species (prey population, x_i) suffer from aboveground natural enemies (predator population, y) and a belowground agents that create an intra-specific mortality (BNDD) dependent on the abundance of the seedling species:

$$\begin{aligned} X_i(k+1) &= X_i(k)e^{b_i - BNDD(X_i(k)) - cY(k)} \\ Y(k+1) &= Y(k)e^{\sum_{i=1}^{n} d_i X_i(k) - eY(k) - r} \end{aligned} \qquad (1.1)$$

As in the traditional Lotka-Volterra model, the seedling population grows (b_i) but is constrained by mortality due to aboveground natural enemies (Y) and a belowground intraspecific mortality (BNDD) that corresponds to a competition term in the traditional Lotka-Volterra system. The main difference in the Lotka-Volterra equations comes from the idea that the value of BNDD is dependent on the abundance of x and is variable over time. Therefore, a new equation needs to be added to the classical case of multi species Lotka-Volterra model that would reflect two important assumed characteristics of BNDD: 1) BNDD is stronger for rare species than for common species and 2) BNDD decreases for rare species but increases for common species

$$BNDD(X_i(k)) = \alpha X_i(k) - X_i^2(k) \tag{1.2}$$

A two-step mechanism

The shift from rarity to commonness is a two-step mechanism. First, as previously discussed, BNDD agents may then shift their target to more common species and soil chemical agents should be secrete by rare species putting them at an advantage compared to common species (by increasing common species BNDD and decreasing rare species BNDD). Thus, BNDD would increase for common species. Because rare species would suffer from fewer aboveground natural enemies (Bachelot and Kobe 201_) and experience decreasing BNDD, their relative abundance would be expected to quickly increase (step A in figure 5.1).

As the abundance of rare species increases, the aboveground natural enemy population can be expected to respond by retargeting the new common species (Bachelot and Kobe 201_). Dietary switch due to food availability occurs frequently in generalist consumers as a way to improve efficiency; mammalian folivores (Shipley and Spalinger 1995, Wiggins et al 2006) but also instars of Leptidoptera species (Barbosa 1978, Barbosa et al 1986, Stephens and Krebs 1986, Roden and Surgeoner 1991, Stoyenoff et al 1994, Singer et al. 2002) have been reported to switch prey. The formerly rare species will thus begin hosting more aboveground natural enemy species and experiencing increased damage and mortality due to aboveground natural enemies. Rare species abundance would then increase less quickly than before aboveground natural enemies had built a response (Step B in Figure 5.1).

From commonness to rarity, part C and D Figure 5.1

Gradual increase in BNDD

Once a rare species has become common, it begins to suffer from many aboveground natural enemies species and its selective advantage decreases. The high diversity of enemies leads to an increase in mortality and, consequently, increased BNDD. Increased BNDD may derive from two ecological processes: Non chemical BNDD agents respond to the increased abundance of the species, and rare species may secrete more anti fungi to decrease mutualistic associations between common species and fungi (Stinson 2006). Both mechanisms should result in a slow increase in BNDD.

A two-step mechanism

When the number of natural enemy species is high, mortality increases (Bachelot and Kobe 201_). Because I assume, as previously discussed, that a plant cannot be well adapted against both high natural enemy richness and BNDD agents, BNDD should progressively increase. This increase in BNDD, associated with a high richness of aboveground natural enemies, results in a fast decline in species abundance until the species has become rare (Part C in Figure 5.1). Once the species become rare enough, aboveground natural enemies are targeting the species less, leading to a slower decline of species abundance (Part D in Figure 5.1).

MATHEMATICAL TEST

Considering the system made by (1.1) and (1.2) previously described and assuming that each suite (b_i, c, d_i, r, α) are strictly positive and respectively confined between (b^l_i,b^u_i), (c^l,c^u), (d^l,d^u), (r^l,r^u), (α^l,α^u) I show that 1) the system is permanent (lemma 1 and 2 in Appendix D), 2) there are stable solutions (lemma 3 in Appendix D), and 3) there exists a stable positive periodic solution. Therefore, from a mathematic point of view, it is possible to obtain cyclic abundance due to aboveground natural enemies and variable negative density dependence.

I first demonstrated that the system (1.3) was permanent, meaning that each seedling host population and enemy community is confined between a maximum and a minimum abundance. No species goes to extinction or to over-dominance. This demonstration is made of lemma 1 and lemma 2. For lemma 1 I demonstrated that each seedling host population and the aboveground enemy population have limits meaning that they do not go extinction and they do not become over- dominant. Then, with lemma 2, I showed that when generation time goes towards infinity, each population tends to equilibrium different from 0 (population non extinct) and different from infinity (population not over-dominant). Theorem 3 (Appendix D) demonstrates the stability of the positive solution; once the system has reached the equilibrium, it remains at the solution even after small disturbance in population abundance. If I managed to prove it from a mathematic point of view, the conditions of stability are hard to obtain in nature. As a result, it should be expected that the host population and enemies coexist via chaotic abundance cycles. This result is not surprising; as it has been shown that demographic process leads to chaos (Dercole et al. 2010).

Once the permanence of the system obtained, I demonstrated that it exists at least one positive stable solution for the system. This is made in the theorem 3. Finally, to support my conceptual model, I proved that one of the positive stable solutions was periodic (theorem 4 in Appendix D). By doing so, I am showing the possibility of obtaining periodic oscillations for each n species of the system under the two forces of aboveground natural enemy and BNDD (Figure 5.2 and 5.3).

DISCUSSION

In the example represented in Figure 5.2, the host species in blue is at an advantage due to a higher growth rate. However, both species are able to coexist in a periodic equilibrium reached around the 500th generation. When increasing the species blue advantage, the system becomes chaotic but remains periodic. I agree that this system is one possible mathematical realization of my conceptual model, but the fact that there is a stable positive periodic solution to it brings support to my conceptual model.

Masters et al.’s (1993) conceptual model proposed that the feedbacks between aboveground and belowground enemies could lead to species coexistence. Their model is fully based on the theory according which belowground enemies positively affect aboveground enemies, while aboveground enemies negatively influence belowground enemies. This model makes the important assumption that all belowground enemies positively influences aboveground enemies through enhance aboveground plant tissue growth, whereas aboveground enemies decreases root tissue growth negatively affecting belowground enemies. If some studies found evidence for such a pattern, others found very differing effect across enemies (see review by Bardgett and Wardle 2010), or the opposite (Bezemer et Dam 2005); in that conceptual model, aboveground enemies enhance root exudates promoting belowground enemies, while belowground enemies increases plant tissue defenses negatively impacting aboveground enemies. Therefore, I am not convinced that a model solely based on the assumption of feedbacks between below and aboveground is accurate enough to explain species abundance.

On the other hand, my model uses the idea of interaction between below and aboveground enemies but adds a temporal dimension allowing the interactions to evolve over different scale: for example, for a rare seedling host, BNDD would decrease faster than aboveground natural enemy richness would increase allowing the host species to increase in abundance.

CONCLUSION

This new conceptual model unifies an aboveground mechanism that follows the CCT with a belowground mechanism that is often opposite to the CCT to explain seedling species coexistence. It is based on two observations that 1) aboveground natural enemy richness leads to differing mortality risk between seedling of rare and common species and 2) conspecific effect on seedling survival is variable of time. It hypothesizes that BNDD should increase for seedlings of common species and decrease for seedlings of rare species. My data did not allow to fully test this idea and future studies should empirically test it.

However, from a mathematical point of view it successfully predicts seedling species coexistence through abundance cycles.

If the conceptual model was defined at a fine ecological scale, I believe it can also be linked to wider variation of BNND over evolutionary time according to the red queen hypothesis: rare species can select better defenses against BNDD agents when suffering from low aboveground natural enemy diversity (Van Valen, 1973). On the other hand BNDD agents could develop better arms against common species when these seedlings experience high aboveground natural enemy richness enabling them to keep developing belowground defenses (Van Valen, 1973). Tying together evolutionary and ecological processes would allow us to understand species coexistence at longer time scale.

Finally, I proposed mechanisms behind BNDD changes, but I did not test them. Future studies should address the variability of BNDD over time. The seed input alternative hypothesis for the variation of NDD should especially be tested.

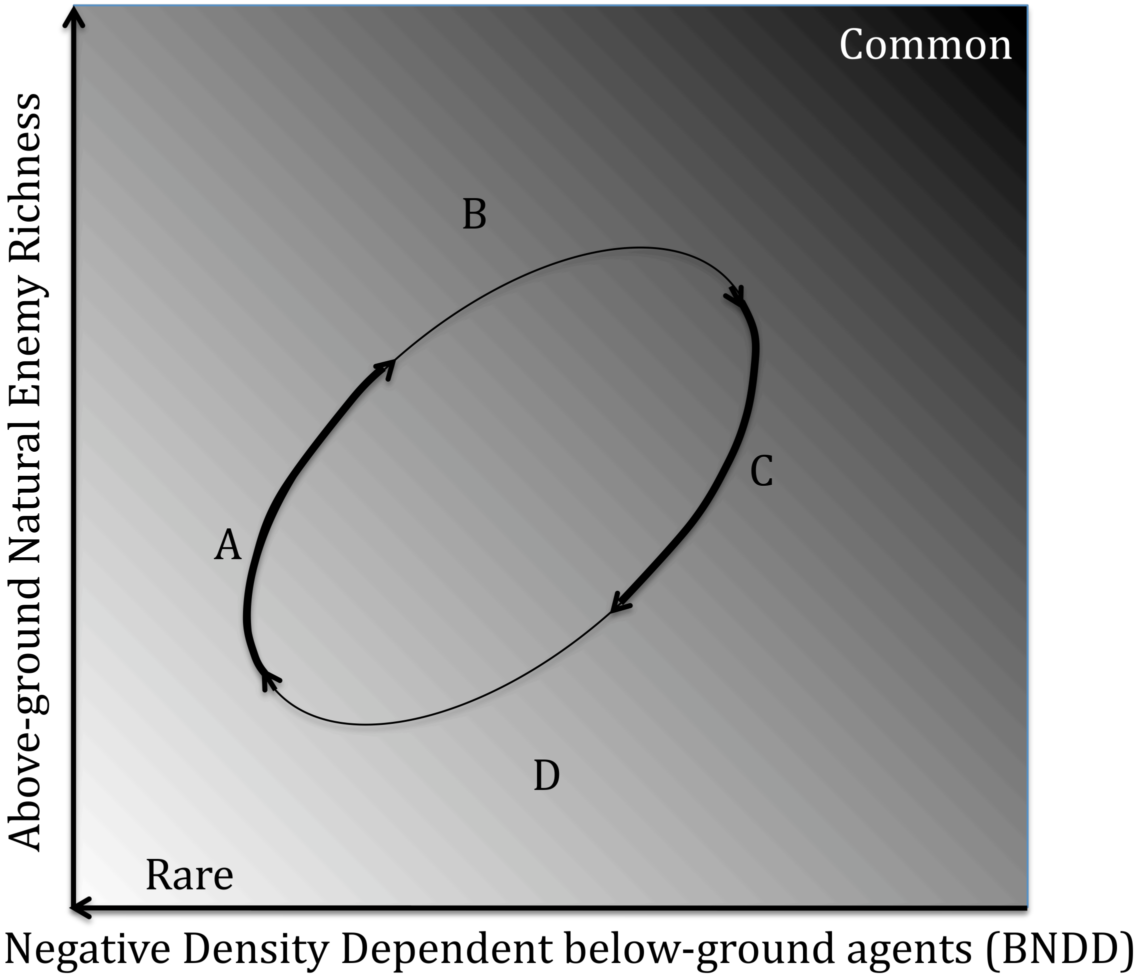
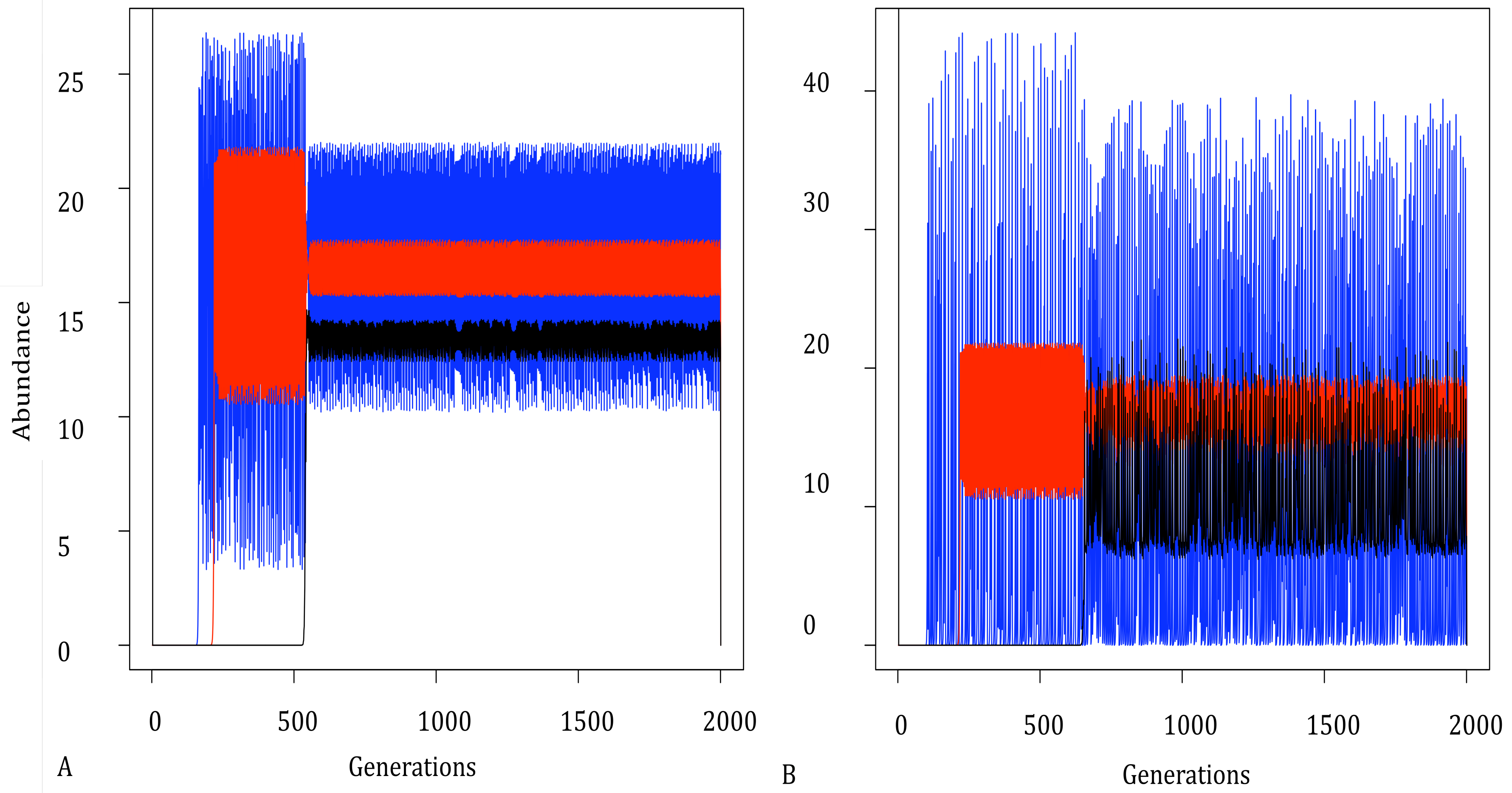


Figure 5.1. Model of change in abundance of a species over time. The light grey area represents when the species is rare. The black area represents when the species is common. A] the species is rare, but increases in abundance because of a lower number of above-ground natural enemy species and change in BNDD. The increase in abundance is quick because the few aboveground enemies. B] The species is now more common, does not experience a high BNDD but there is a lagging increase in the number of aboveground natural enemies. Thus, the increase in abundance is slow. C] The aboveground natural enemies had enough time to build up a response. BNDD increase, abundance drops. D] the species became rare, BNDD is high but very few above-ground natural enemies, the abundance decreases more slowly.

Figure 5.2. Examples of equilibrium reached by the mathematical model in the case of two seedlings species (the blue and the red) and above ground natural enemy population (black): On the right (A), the blue seedlings have a growth advantage of 33% compared to the red seedlings (b_1=0.8344). On the left (B), the blue population has a growth advantage of 112% compared to the red host, the equilibrium is periodic but chaotic (b_1=1.3344). b_2=0.6281, α=0.6332, c=0.2369, d_1=0.3700, d_2=0.9098, e=0.8161, r=0.1403. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.



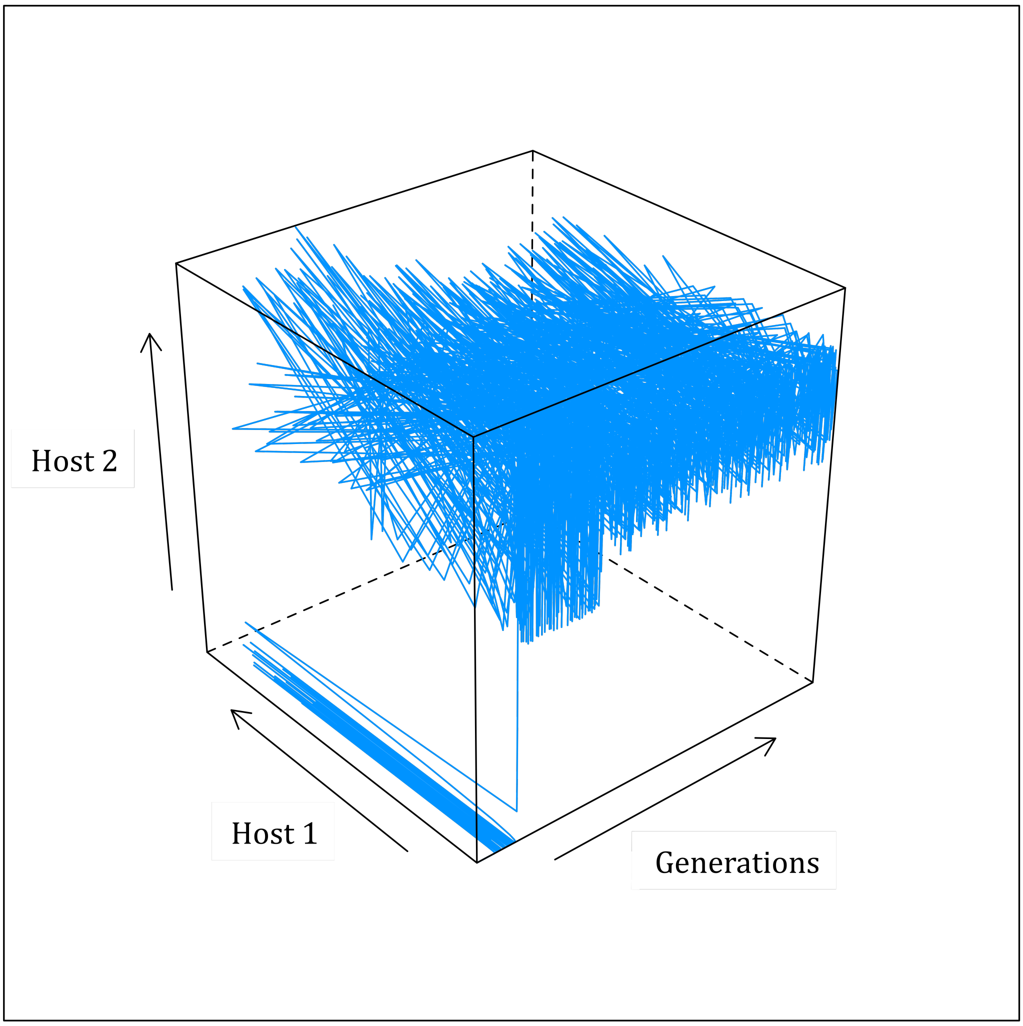


Figure 5.3. Evolution of the abundance of seedling species 2 (Host 2), function of seedling species 1 (Host 1) over generation time. Case B of Figure 5.2. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

LITERATURE CITED

LITERATURE CITED

Anderson, R. M. and R. M. May, 1992. Infectious Diseases of Humans, Dynamic and Control. Oxford University Press, Oxford.

Augspurger, C. K., 1983. Offsping recruitment around tropical trees-Changes in cohort distance with time. Oikos 40, 189-196.

Augspurger, C. K., 1983. Seed dispersal of the tropical tree, Platypodium elegans, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71, 759-771.

Augspurger, C. K., 1984. Seedling survival of tropical tree species-Interations of dispersal distance, light gaps, and pathogens. Ecology 65, 1705-1712.

Bachelot, M. P. E., and R. K. Kobe, 201_. Do seedlings of common tropical tree species host more natural enemy species than seedlings of rare neotropical tree species? A new interpretation of the Janzen-Connell hypothesis. In prep

Bachelot, M. P. E., and R. K. Kobe, 201_. Advantage and Disadvantage of being a rare tropical seedling in a wet tropical lowland forest. In prep

Barbosa, P., 1978. Host pant exploitation by the gypsy moth Lymantria dispar. Entomologia experimentalis et applicata, 24, 28-37.

Barbosa, P., P. Martinat, and M. Waldvogel, 1986. Development, fecundity and survival of the herbivore *Lymantria dispar* and the number of plant species in its diet. Ecological Entomology, 11, 1-6.

Bardgett, R. D., 2005. The biology of soil: a community and ecosystem approach. Oxford University Press, New York.

Bardgett, R. D. and D. A. Wardle, 2010. Aboveground-belowground linkages. Biotic interactions, ecosystem processes, and global change. Oxford series in ecology and evolution, New York.

Bever, J. D., 2002. Host-specificity of AM fungal population growth rates can generate feedback on plant growth. Plant and Soil 244, 281-290.

Berryman, A., 2002. Population cycles - The case for trophic interactions. New York, Oxford University Press.

Boutin, S., C. J. Krebs, R. Boonstra, A. R. E. Sinclair and K. E. Hodges, 2002. Understanding the snowshoe Hare Cycle trhough Large-scale Field Experiments. In Population Cycles – The case for trophic interactions. New York, Oxford University Press.

Brown, V. K. and A. C. Gange, 1989. Differential effect of above-ground and below-ground insect herbivory during early succession. Oikos, 54, 67-76.

Castelli, J. P. and B. B. Casper, 2003. Intraspecific AM fungal variation contributes to plant-fungal feedback in a serpentine grassland. Ecology 84, 323-336.

Chen, F. D., 2006. Permanence and global attractivity of a discrete multispecies Lotka-Volterra competition predator-prey systems. Applied Mathematics and Computation 182, 3-12.

Clark, D. A. and D. B. Clark, 1984. Spacing dynamics of a tropical rain-forest tree-Evaluation of the Jazen-Connell model. American Naturalist 124, 769-788.

Comita, L. S., H. C. Muller-Landau, S. Aguillar, and S. P. Hubbell, 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329, 330-332.

Connell, J. H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. 298 312 in P. J. D. Boer and G. R. Gradwell, editors. Dynamics of numbers inpopulations. Centre for Agricultural Publication and Documentation,Wageningen, Netherlands.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non equilibrium state. Science, 199, 1302-1310.

Connell, J. H., J. G. Tracey, L. J. Webb, 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. Ecological Monographs, 54, 141-164.

De Deyn, G. B., and W. H. Van der Putten, 2005. Linking aboveground and belowground diversity. Trends in Ecology and Evolution, 20, 625-633.

Dercole, F., R. Ferriere, and S. Rinaldi, 2010. Chaotic Red Queen coevolution in three-species food chains. Proceedings of the Royal Society B-Biological Sciences, 277, 2321-2330.

Ehrenfeld, J. G., B. Ravit, and K. Elgersma, 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources 30, 75-115.

Elton, C. S., 1942. Voles, mice and lemmings. Claredon Press, Oxford.

Ferriere, R. and B. Cazelles, 1999. Universal power laws govern intermittent rarity in communities of interacting species. Ecology, 80, 1505-1521.

Ferriere, R., A. Guionnet, and I. Kurkova, 2006. Timescales of population rarity and commonness in random environments. Theoretical Population Biology, 69, 351-366.

Fritz, R. S., and E. L. Simms, 1992. Plant resistance to her- bivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago.

Gilbert, G. S., K. E. Harms, D, N, Hamill, and S. P. Hubbell, 2001. Effects of seedling size, El Nino drought, seedling density, and distance to nearest conspecific adult on 6-year survival of Ocotea whitei seedlings in Panama. Oecologia, 127, 509-516.

Hallett, S. G., D. Prati, and J. N. Klironomos, 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. Plos Biology 4, 727-731.

Hammond D.S., and V. K. Brown, 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell, Oxford, 51-78.

Hanski, I., 1985. Single-species spatial dynamics may contrivute to long-term rarity and commonness. Ecology, 66, 335-343.

Hanski, I. and H. Henttonen, 2002. Population cyles of small rodents in Fennoscandia. In Population cycles – The case for trophic interactions. New York, Oxford University Press.

Hoshizaki, K., S. Wajirou, and S. satohiko, 1997. Impacts of secondary seed dispersal and herbivory on seedling survival in *Aesculus turbinata*. Journal of Vegetation Science, 8, 735-742.

Howe, H. F., 1990. Survival and growth of juvenile Virola surinamensis in Panama-effects of herbivory and canopy closure. Journal of Tropical Ecology, 6, 259-280.

Hudson, P. J., A. P. Dobson, and D. Newborn, 2002. Parasitic worms and population cycles of red grouse. In Population cycles – The case fro trophic interactions. Oxford University Press, New York.

Hutchinson, G. E., 1948. Circular causal systems in ecology. Annals of the New York Academy of Sciences 50, 221-246.

Janzen, D. H., 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104, 501-528.

Jones, D. L., and J. H. Lawton, 1995. Linking species and ecosystems. Chapman and Hall, New York.

Klironomos, J. N., 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417, 67-70.

Lawton, J. H., 1994. What do species do in ecosystems? Oikos, 71, 367-374.

Lotka, A. J., 1925. Elements of Physical Biology, Williams and Wilkins, Baltimore.

MacArthur, R. H ., 1958. Populationecology of some warblers in northeastern coniferous forests. Ecology, 39, 599-619.

MacArthur, R.H., 1968. The theory of the niche. In Population Biology and Evolution (Lewontin, R., ed.), 159–176, Syracuse University Press.

MacArthur R., 1970. Species packing and competitive equilibrium for many species. Theor. Popul. Biol, 1,1–11.

Mangan, S. A., E. A. Herre, and J. D. Bever, 2010a. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant-soil feedback. Ecology 91, 2594-2603.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever, 2010b. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466, 752-U710.

Masters, G. J., V. K. Brown, and A. C. Gange, 1993. Plant mediated interactions between boveground and belowground insect herbivores. Oikos, 66, 148-151.

McCarthy-Neumann, S. and R. K. Kobe, 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. Ecology, 89, 1883-1892.

Mueller, L. D., 1997. Theoretical and empirical examination of density-dependent selection. Annual Review of Ecology and Systematics 28, 269-288.

Munster-Swendsen, M., 2002. The role of insect parsitoids in populations cycles of spruce needleminer in Denmark. In Population cycles – the case for trophic interactions. New York, Oxford University Press.

Packer, A. and K. Clay, 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404, 278-281.

Peters, H. A., 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. Ecology Letters 6, 757-765.

Pitelka, F. A., 1957. Some aspects of population structure in the short-term cycle of the brown lemming in northern Alaska. Cold Spring Harbor Symposia on Quantitative Biology, 22, 237-251.

Reeve, J. D. and P. Turchin, 2002. Evidence for predator-prey cycles in a bark beetle. In Population cycles – The case for trophic interactions. New York, Oxford Press University.

Roden, D. B. and G. A. Surgeoner, 1991. Survival, devlopment time, and pupal weights of larvae of gypsy moth reared on foliage of common trees of the upper Great Lakes region. Northern Journal of Applied Forestry, 8, 126-128.

Rosenzweig, M. L. and M. V. Molino, 1997. Who gets the short bits of the broken stick? In K. Gaston and W. E. Kunin, editors. Rarity in biological systems. Chapman and Hall, London

Schupp, E. W., 1988. Factors affecting post-dispersal seed survival in a tropical forest. Oecologia 76, 525-530.

Schupp, E. W., 1992. The Janzen-Connell model for tropical tree diversity-Pooulation implications and the importance of spatial scale. American Naturalist 140, 526-530.

Shipley, L. A. and D. E. Spalinger, 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. Oecologia, 104, 112-121.

Singer, M. S., E. A. Bernays, and Y. Carriere, 2002. The interplay between nutrient balancing and toxin dilution in foraging by a generalist insect herbivore. Animal Behaviour, 64, 629-643.

Stephens, D. W., and J. R. Krebs, 1986. Foraging theory. Princeton University Press, Princeton

Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, Terborgh, J., N. Pitman, M. Silman, H. Schichter, and V. P. Nunez, 2002. Maintenance of tree diversity in tropical forests. Seed dispersal and frugivory: ecology, evolution and conservation. Third International Symposium-Workshop on Frugivores and Seed Dispersal, Sao Pedro, Brazil, 6-11 August 2000, 1-17.

Stoyenoff, J. L., J. A. Witter, M. E. Montgomery and C. A. Chilcote, 1994. Effects of host switching on gypsy moth *(lymantria dispar* (L.)) under field conditions. Oecologia, 97, 143-157.

Travis, J., 1990. The interplay of population-dynamics and the evolutionary process. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 330, 253-259.

Valen L. V., 1973. A new evolutionary law. Evolutionary Theory, 1, 1-30.

Valencia, R., H. Balslev, and G. Paz y Miño, 1994. High tree alpha-diversity in amazonian ecuador. Biodiversity and Conservation 3, 21-28.

Vandermeer, J., 1982. To be rare is to be chaotic. Ecology 63, 1167-1168.

Vandermeer, J., 1993. Loose coupling predator-prey cycles- Entrainment, chaos, and intermittency in the classic Macarthur consumer-resource equations.. American Naturalist 141, 687-716.

Vitousek, P. M., and L. R. Walker, 1989. Biological invasion by Myerica faya in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecoslogical Monographs, 59, 247-265.

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118, 558-560.

Wardle, D. A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton, NJ.

Webb, C. O. and D. R. Peart, 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology 80, 2006-2017.

Wiggins, N. L., C. McArthur, and N. W. Davies , 2006. Diet switching in a generalist mammalian folivore: fundamental to maximising intake. Oecologia, 147, 650-657.

Wills C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, R. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. Loo de Lao, M. Massa, C. Nath, Md. Nur Supardi Noor, A. Rahman Kassim, R. Sukumar, H. Satyanarayana Suresh, I. Sun, S. Tan, T. Yamakura, J. Zimmerman, 2006. Nonrandom processes maintain diversity in tropical forests. Science, 311, 527-531.

CHAPTER VI

CONCLUSIONS

Understanding differing seedling mortality across tropical tree species is an important step toward understanding the maintenance of tropical tree species diversity. At a time when global warming and human practices threaten highly diverse ecosystems, it is crucial to combine our efforts to answer the tropical ecologist's challenge of explaining the mechanisms behind high alpha tree diversity. By understanding these mechanisms, foresters and managers will be better able to conserve or restore these ecosystems. If in this research I do not study or propose conservation and restoration practices, I tackle one of the most widely acknowledged hypotheses proposed to explain the high alpha tree diversity in the tropics: the Janzen-Connell hypothesis. However, rather than testing the JC in a conventional way, I first approached it from an aboveground natural enemy richness and a community compensatory trend (CCT) point of view. Overall, the second chapter of my work demonstrated that according to my expectations, seedlings of common tree species host a higher diversity of natural enemies than seedlings of rare tropical tree species. In chapter three, this finding was then linked to a higher mortality in common species than in rare species. Taken together, the results bring strong support for both the new facet of the JC and the CCT. It is important to note that the impact of natural enemy richness on seedling mortality was negative solely for the youngest seedlings. Therefore, the support of the JC and the CCT from an aboveground natural enemy's perspective applies to the earliest stage of the seedlings. Furthermore, my results were consistent with the JC solely from a density perspective but failed to detect a distance from adult tree effect: species that tend to disperse closer to parent trees did not seem to host higher natural enemy diversity. This could result from an artifact of high variation in distance from adult tree within species or it could be the result of highly differential leaf morphology, leading to different natural enemies between seedlings and mature trees.

Interestingly, aboveground natural enemy diversity also increases with relatedness of the neighbor. These results emphasize the importance of looking beyond the notion of "conspecific versus heterospecific". I acknowledge the weakness of my phylogenetic signal partly due to the old average time of divergence between species present in the transects. However, further work is needed to understand how phylogeny, traits involved in natural enemy defense, and natural enemy richness are correlated. Shade tolerance was positively correlated with natural enemy diversity. This result was in contradiction with my expectation, but supports previous studies that found higher amount of damage in shade than in the sun. Because shade species preferentially occur in low light environments they could encounter more natural enemies.

In the third chapter, I also evaluate the effect of conspecific neighbors on seedling survival, a more conventional way of addressing the JC. Interestingly, my study showed a different result than when looking at seedling mortality from an aboveground natural enemy richness perspective. If seedlings of rare species are at an advantage from an aboveground perspective, conspecific neighbors disadvantage them compared to seedlings of common species. However, when testing for temporal variation in conspecific effect on seedling survival, I demonstrated that conspecific neighbors equally affect seedlings of rare and common species 41 % of the time while placing seedlings of rare species at an advantage compared to seedlings of common species 6 % of the time. To my knowledge this is the first test and evidence that conspecific effect changes over time.

To summarize the third chapter, aboveground natural enemy richness acts according to the compensatory trend theory and can thereby enhance species coexistence. However, NDD acts more often against CCT by disadvantaging rare species more than common species. In order to reconcile the two forces, I proposed a conceptual model of community seedling abundance in the fourth chapter. If more empirical work is needed to assess the validity of the model, my first mathematic test and previous empirical findings bring positive initial support. First, one mathematic realization of the systems proved the existence of a stable positive periodic solution: species could coexist via abundance fluctuations. Second, the assumption that high natural enemy richness leads to high mortality was validated in the third chapter. Finally, NDD was variable over time bringing some evidence that BNND may be also variable over time. A better understanding of BNND and of its variability over time is needed in order to bring more evidence in favor of or against my conceptual model. Finally, because damage impacts seedling mortality solely at the young seedling stage, more work is necessary to adapt the conceptual model to later life stages and fully test the effect of abundance fluctuations on species coexistence.

This novel assessment of one of the most famous theories to explain the high alpha tree diversity in the tropics, the Janzen-Connell hypothesis, offered some new insights to understand species coexistence (aboveground natural enemies disadvantage seedlings of common species, and conspecific effect does not always disadvantage seedlings of rare species). It is my hope that future studies will follow my Master research and further link aboveground and belowground mechanisms within a temporal framework (ecological and evolutionary time) in an effort to understand species coexistence.

APPENDIX A

Table A.1. Example of table of damage patterns for *Brosimum lactescens*

		Damage ID										
Species	**ID**	1	2	3	4	5	6	7	8	9	10	11
Brosimum_lactescens	25497	1	1									
Brosimum_lactescens	24972			1	1	1	1					
Brosimum_lactescens	22762		1	1			1	1	1	1	1	
Brosimum_lactescens	25463						1					1

Table A.2. Description of the different variables

Variables	**symbol**	**type**
average conspecific seedling density over the past 10 years	D	Community
average conspecific density in January 2010	d	Community
average conspecific density over the past 1 year, 2 year … 9 years	d1, d2… d9	Community
conspecific tree density	T	Community
tree basal area	BA	Community
average number of adult occurring within a 20 meters radius	T20	Community
average local phylogenetic distance	dp	Community
average local phylogenetic distance without conspecifc	dpH	Community
the distance to the closest conspecific adult tree	Dist	Community
average irradiance	I	Abiotic
average moisture	M	Abiotic
average air humidity	m	Abiotic
average total nitrogen	Nnet	Abiotic
average net mineralization	Ntot	Abiotic
average total carbon	Ctot	Abiotic
average base cations sum	B	Abiotic
average phosphorus	P	Abiotic
average lifespan	L	Biotic
probability of mortality under 1; 2 or 0.5% of light without conspecific adult	ST	Biotic

Table A.3 Results of the Michaelis Menten model for the 44 species

Species	N	Asymptote (sd)	K (sd)	r^2 (%)
Anaxagorea crassipetala	30	48,55 (0.15)	10,83 (0.09)	0,94
Ardisia nigropunctata	8	28,03 (0.47)	3,27 (0.12)	0,66
Astrocaryum confertum	3	12,15 (4.18)	2,41 (1.48)	0,86
Borojoa panamensis	12	35,13 (0.17)	6,15 (0.06)	0,59
Brosimum lactescens	4	24,37 (4.48)	4,29 (1.24)	0,64
Byrsonima crispa	5	34,84 (1.83)	3,22 (0.32)	0,79
Capparis pittieri	13	16,18 (0.12)	6,33 (0.1)	0,42
Casearia arborea	3	8,00 (1.77)	1,00 (0.59)	0,47
Coussarea hondensis	17	66,23 (0.04)	9,46 (0.01)	0,6
Coussarea talamancana	4	29,90 (3.31)	3,43 (0.64)	0,47
Cryosophila warscewczii	4	20,57 (2.86)	3,00 (0.74)	0,6
Cupania pseudostipularis	3	27,14 (7.18)	3,80 (1.53)	0,45
Dendropanax arboreus	4	11,24 (3.8)	3,73 (2.08)	0,33
Euterpe precatoria	15	18,96 (0.04)	4,41 (0.02)	0,52
Faramea multiflora	3	21,46 (4.07)	2,41 (0.81)	0,46
Faramea parvibractea	3	25,53 (4.22)	2,49 (0.72)	0,82
Guarea guidonia	12	41,43 (0.19)	6,65 (0.06)	0,5
Guatteria aeruginosa	5	10,96 (2.80)	4,53 (1.90)	0,46
Guatteria diospiroides	12	18,08 (0.20)	7,17 (0.15)	0,53
Hampea appendiculata	6	51,39 (2.57)	6,47 (0.50)	0,57
Hernandia didymantha	12	72,77 (0.24)	8,25 (0.05)	0,7
Hirtella lemsii	3	20,35 (4.55)	2,64 (1.01)	0,78
Inga thibaudiana	4	28,44 (5.12)	4,78 (1.31)	0,55
Iriartea deltoidea	12	49,73 (0.22)	7,61 (0.06)	0,77
Lacmellea panamensis	19	43,46 (0.02)	9,32 (0.01)	0,57
Neea elegans	3	18,95 (2.75)	1,69 (0.51)	0,91
Neea psychotrioides	5	21,34 (1.72)	3,12 (0.48)	0,68
otoba novogranatensis	4	45,66 (9.92)	7,53 (2.19)	0,88
Paragonia Pyramidata	9	40,52 (0.76)	7,47 (0.23)	0,58
Pentaclethra macroloba	42	21,16 (0.05)	4,35 (0.05)	0,85
Perebea hispidula	4	23,06 (3.55)	3,63 (0.93)	0,68
Pholidostachys pulchra	9	34,11 (0.38)	4,13 (0.10)	0,71
Posoqueria posoqueria verdegruesa	3	28,89 (2.91)	1,79 (0.36)	0,62
Pourouma bicolor	22	44,18 (0.01)	8,79 (0.002)	0,52
Prestoea decurrens	9	42,22 (0.55)	5,77 (0.14)	0,48
Protium panamense	5	31,83 (3.19)	5,12 (0.81)	0,61
Psychotria panamensis	32	53,18 (0.13)	10,69 (0.07)	0,93
Quina schippii	6	34,60 (1.78)	4,89 (0.42)	0,83
Rinorea deflexiflora	23	49,77 (0.17)	6,83 (0.06)	0,92
Simarouba amara	5	35,04 (1.25)	2,28 (0.18)	0,72

Table A.3. (cont'd)

Socratea exorrhiza	7	41,11 (1.24)	5,35 (0.28)	0,88
Tapirira myriantha	8	36,48 (0.45)	3,16 (0.09)	0,62
Virola koschnyi	7	37,65 (0.68)	3,09 (0.12)	0,79
Virola sebifera	14	39,12 (0.07)	5,59 (0.02)	0,46

Species	Lifespan	Average conspecific density	Irradiance	Moisture	Total N	Total C	Net N	N min	PO4	Base cation	N. phylogenetic index	Distance from adult	Tree in 20m
Anaxagorea crassipetala	0.03* (-) 43%	0.08	0.7	0.4	0.4	0.9	0.08	0.1	0.2	0.6	0.2	0.03* (+) 43%	0.08
Pentaclethra macroloba	0.6	0.2	1	0.4	0.2	0.09	0.1	0.2	0.6	0.1	0.8	0.8	0.2
Pourouma bicolor	0.8	0.4	0.4	0.8	0.5	0.3	0.5	0.4	0.2	0.9	0.07	0.5	0.4
Psychotria panamensis	0.6	0.7	0.2	0.9	0.3	0.4	0.6	0.9	0.7	0.4	0.8	0.9	0.7
Rinorea deflexiflora	0.01* (+) 38%	0.9	0.5	0.8	0.9	1	0.8	0.7	0.06	0.05* (-)27%	0.4	0.6	0.9

Table A.4. Results of the species-specific linear regression of the number of foliar natural enemy species hosted by an individual against each variable. * means that the variable has a significant effect. (-) stands for a negative correlation. (+) represents a positive relation. The percentage is the r^2.

Table A.5. 32 selected species for the community model with the three important factor: global abundance, shade intolerance and phylogenetic index

Species	Asymptote	Phyloseedling	ShadeTolerance1	year5
Anaxagorea crassipetala	48.55	66.97	0.18	2.90
Ardisia nigropunctata	28.03	159.25	0.12	0.23
Brosimum lactescens	24.37	43.77	0.15	0.92
Byrsonima crispa	34.84	144.40	0.12	0.37
Capparis pittieri	16.18	18.31	0.29	1.63
Coussarea hondensis	66.23	76.55	0.15	7.86
Coussarea talamancana	29.90	61.99	0.09	0.01
Dendropanax arboreus	11.24	81.38	0.25	0.31
Euterpe precatoria	18.96	148.76	0.10	0.28
Faramea parvibractea	25.53	92.63	0.13	0.96
Guarea guidonia	41.43	84.78	0.10	0.03
Guatteria diospiroides	18.08	170.95	0.20	0.37
Hampea appendiculata	51.39	71.74	0.18	2.40
Hernandia didymantha	72.77	71.36	0.05	2.04
Hirtella lemsii	20.35	219.70	0.07	0.29
Inga thibaudiana	28.44	107.29	0.07	0.17
Iriartea deltoidea	49.73	118.51	0.03	1.06
Lacmellea panamensis	43.46	75.49	0.10	0.70
Neea elegans	18.95	185.67	0.08	0.06
Neea psychotrioides	21.34	78.47	0.24	0.10
Perebea hispidula	23.06	121.44	0.09	0.09
Pholidostachys pulchra	34.11	95.93	0.08	1.36
Pourouma bicolor	44.18	99.73	0.09	2.40
Prestoea decurrens	42.22	96.60	0.13	1.77
Protium panamense	31.83	116.87	0.08	1.32
Psychotria panamensis	53.18	101.49	0.25	0.83
Rinorea deflexiflora	49.77	135.98	0.10	3.91
Simarouba amara	35.04	106.23	0.18	0.96
Socratea exorrhiza	41.11	80.76	0.02	0.94
Tapirira myriantha	36.48	69.41	0.23	1.25
Virola koschnyi	37.65	155.17	0.05	1.17
Virola sebifera	39.12	136.79	0.06	1.35

Table A.6 models comparing the effect of species abundance when calculated over different time periods.

Time period	i+ a*Abundance		AIC	d(AIC)	r^2 (%)
	i (sd)	a (sd)			
0 year	29 (2.6)	257.6 (58.6)	226.8	1.6	41.8
1 year	28.((2.7)	29.8 (7.2)	228.2	3	38.9
2 years	30.3 (2.6)	14.0 (3.5)	229.3	4.1	36.6
3 years	29.1 (2.8)	10.8 (2.7)	229.1	3.9	37.0
4 years	28.1 (2.7)	8.3 (1.8)	225.5	0.3	44.3
5 years	**28.5 (2.6)**	**6.2 (1.3)**	**225.2**	**0**	**45.0**
6 years	28.5 (2.6)	5.4 (1.2)	225.5	0.3	44.3
7 years	29.0 (2.6)	4.4 (1.0)	226.6	1.4	42.1
8 years	28.9 (2.6)	4.0 (0.9)	226.6	1.4	42.2
9 years	28.5 (2.6)	3.7 (0.8)	226.1	0.9	43.2
10 years	28.5 (2.8)	3.0 (0.7)	227.7	2.5	40.0

Table A.7 models comparing the effect of phylogenetic index when calculated over different time periods.

Time period	i+ a*Phylogenetic Index		AIC	r^2 (%)
	i (sd)	a (sd)		
0 year	**50 (7.5)**	**-0.13 (0.06)**	**239**	**12**
1 year	45 (12)	n.s	242	2
2 years	44 (13)	n.s	242	2
3 years	43(15)	n.s	242	2
4 years	46 (14)	n.s	242	1
5 years	45 (14)	n.s	242	**1**
6 years	44 (14)	n.s	242	1
7 years	42 (14)	n.s	242	1
8 years	40 (14)	n.s	242	0
9 years	36 (14)	n.s	242	0
10 years	36 (14)	n.s	242	0

Table A.8. Distributions of the estimated natural enemy richness among species via 1000 resampling. The Asymptote represents the Nd_{max} estimated with the entire data set.

	Confidence intervals			
Species	**Median**	**Lower**	**Upper**	**Asymptote**
Anaxagorea crassipetala	47.54	30.60	73.93	48.55
Ardisia nigropunctata	23.21	19.37	27.97	28.03
Astrocaryum confertum	15.95	15.95	15.95	12.15
Borojoa panamensis	27.40	18.66	36.81	35.13
Brosimum lactescens	28.99	28.99	36.96	24.37
Byrsonima crispa	31.78	29.62	35.17	34.84
Capparis pittieri	19.83	13.26	29.61	16.18
Casearia arborea	7.59	7.59	7.59	8.00
Coussarea hondensis	36.87	28.22	47.92	66.23
Coussarea talamancana	35.65	29.15	39.65	29.90
Cryosophila warscewczii	23.95	20.00	34.09	20.57
Cupania pseudostipularis	34.09	34.09	34.09	27.14
Dendropanax arboreus	19.83	19.83	29.61	11.24
Euterpe precatoria	16.44	12.33	26.51	18.96
Faramea multiflora	23.43	23.43	23.43	21.46
Faramea parvibractea	27.51	27.51	27.51	25.53
Guarea guidonia	27.36	21.38	35.35	41.43
Guatteria aeruginosa	19.83	13.26	22.21	10.96
Guatteria diospiroides	19.83	8.22	29.61	18.08
Hampea appendiculata	69.52	39.77	91.98	51.39
Hernandia didymantha	72.32	50.19	95.08	72.77
Hirtella lemsii	23.21	23.21	23.21	20.35
Inga thibaudiana	39.65	36.96	39.65	28.44
Iriartea deltoidea	52.74	39.44	74.03	49.73
Lacmellea panamensis	27.67	19.40	39.77	43.46
Neea elegans	19.28	19.28	19.28	18.95
Neea psychotrioides	24.05	20.55	32.75	21.34
Otoba novogranatensis	64.36	39.77	84.29	45.66
Paragonia Pyramidata	34.24	23.95	51.82	40.52
Pentaclethra macroloba	15.78	12.43	19.40	21.16
Perebea hispidula	47.54	23.59	84.29	23.06
Pholidostachys pulchra	38.94	31.13	49.77	34.11
Posoqueria posoqueria verdegruesa	29.28	29.28	29.28	28.89

Table A.8 (cont'd)

Pourouma bicolor	31.13	23.43	40.00	44.18
Prestoea decurrens	48.11	39.22	88.84	42.22
Protium panamense	39.65	32.07	55.47	31.83
Psychotria panamensis	36.87	26.99	59.09	53.18
Quina schippii	45.89	32.75	64.36	34.60
Rinorea deflexiflora	39.97	31.48	53.77	49.77
Simarouba amara	35.19	30.35	42.48	35.04
Socratea exorrhiza	44.81	34.09	55.46	41.11
Tapirira myriantha	34.62	25.31	42.48	36.48
Virola koschnyi	33.25	27.97	44.81	37.65
Virola sebifera	44.73	36.81	57.70	39.12

Table A.9 Results of the regression between the median, the lower and the upper estimates of Nd_{max} against the three previously selected factors.

Nd estimates	***Factors***	**Estimates**	**Standard error**	**p value**	**R^2 (%)**
Lower boundaries	Intercept	40.93	5.64	< 0.001	48
	Abundance	3.47	1.38	< 0.05	
	Shade tolerance	-73.83	19.32	< 0.001	
	Phylogenetic index	-0.07	0.03	< 0.05	
Median	Intercept	51.40	8.67	< 0.001	46
	Abundance	6.36	2.12	< 0.01	
	Shade tolerance	-88.14	29.72	< 0.01	
	Phylogenetic index	-0.11	0.05	< 0.05	
Upper boundaries	Intercept	63.94	14.67	< 0.001	37
	Abundance	10.17	3.59	< 0.01	
	Shade tolerance	-93.64	50.27	< 0.01	
	Phylogenetic index	-0.14	0.08	~ 0.11	

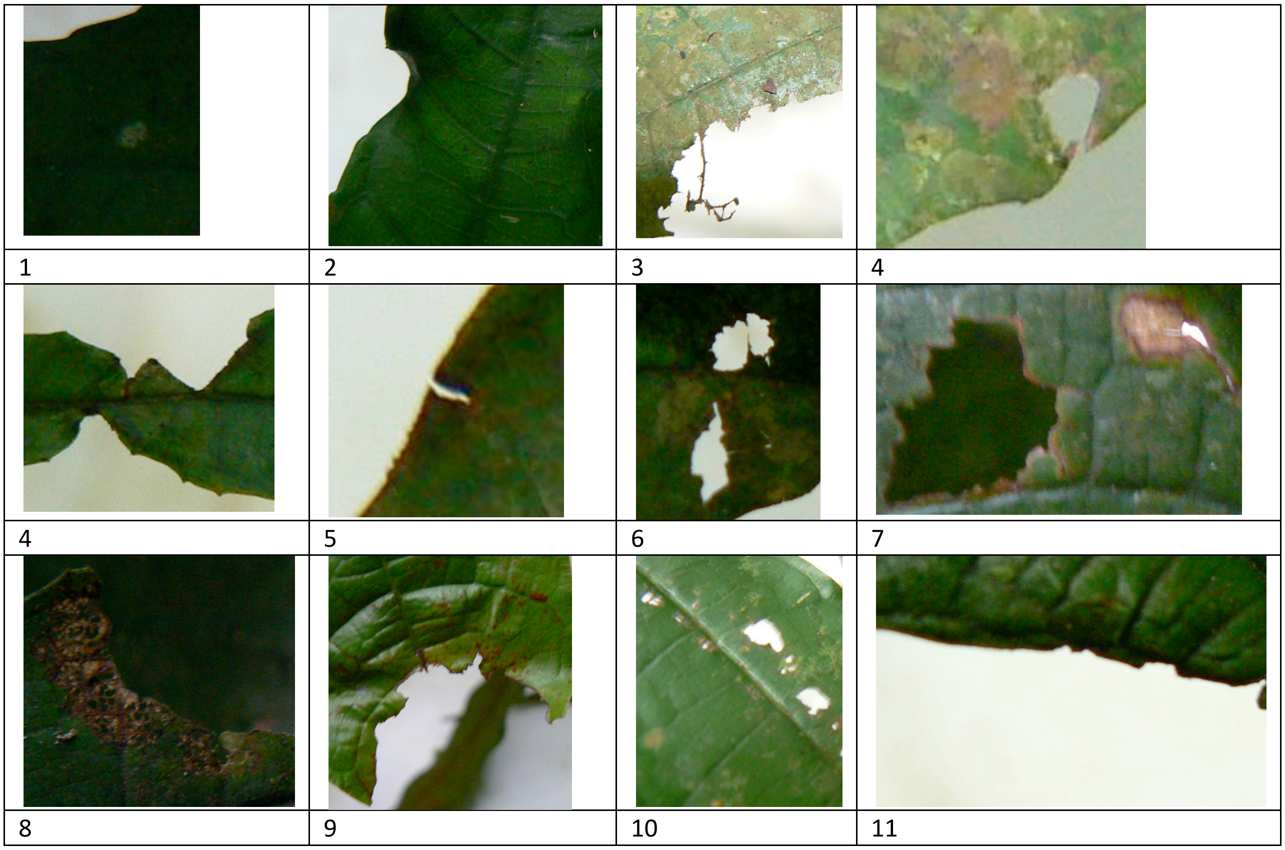


Figure A.1. Example of damage patterns for *Brosimum lactescens.* For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis

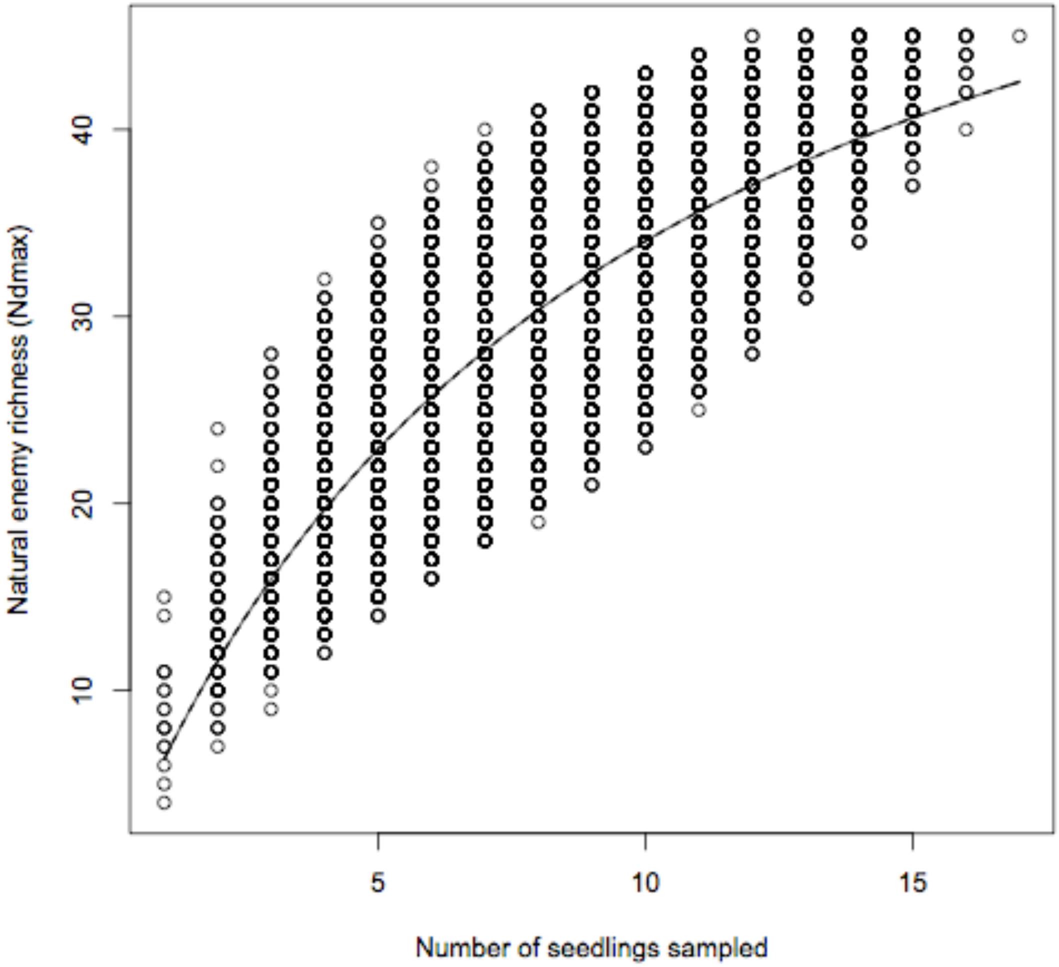


Figure A.2. Example (Coussarea hondensis) of cumulative number of damage patterns, a proxy for natural enemies richness, as a function of increasing seedling-sampling effort. Curve represents the Michaelis-Menten function. Ndmax represents the expected number of damage types found for this species. K stands for the number of seedlings for which half of the number of damage patterns would be found.

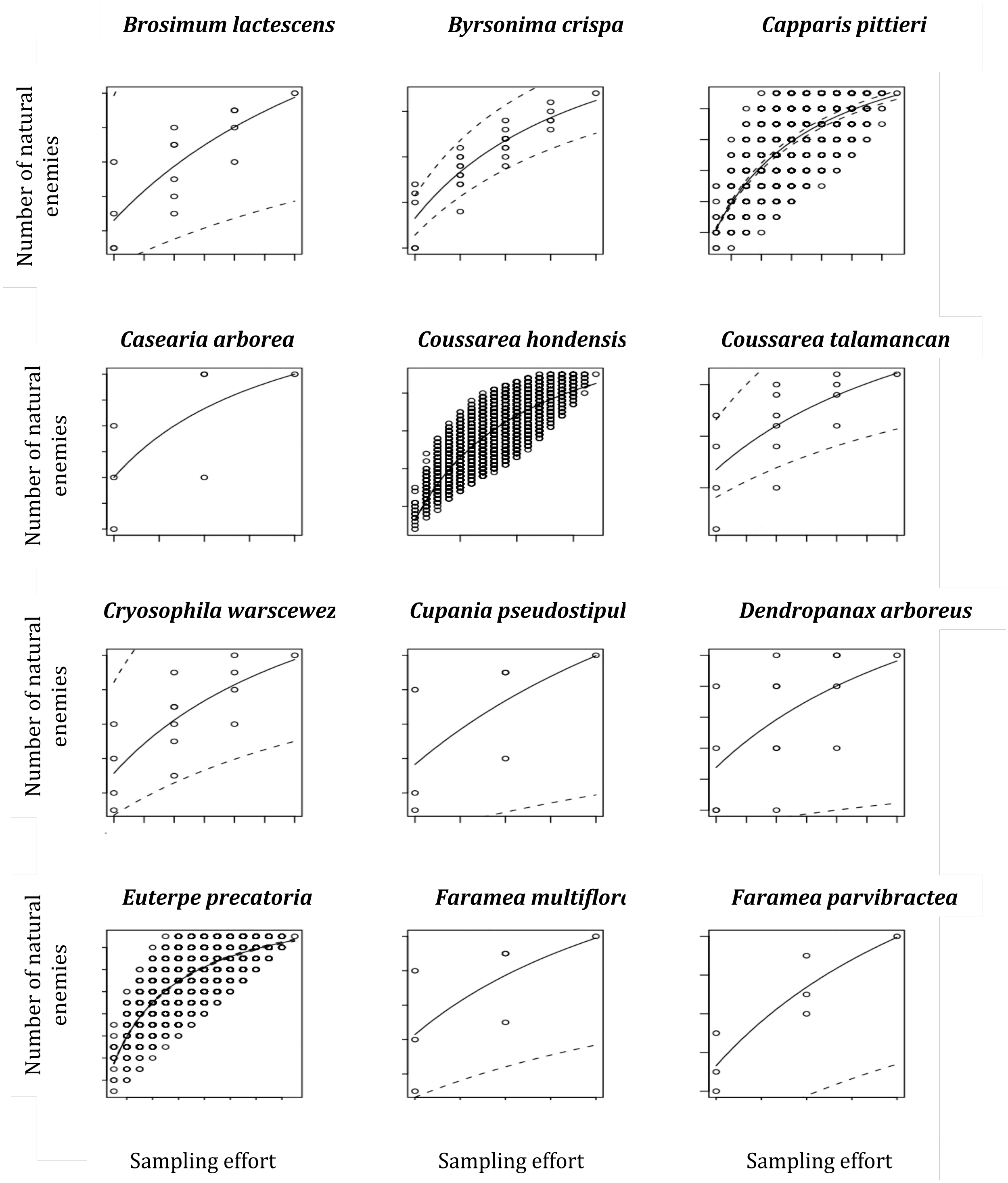


Figure A.3. Rarefaction curves for the 44 species. Sampling effort represents the number of individual seedling used to assess the number of different damage (proxi for Natural enemy species) on the y-axis.

Figure A.3. (cont’d)

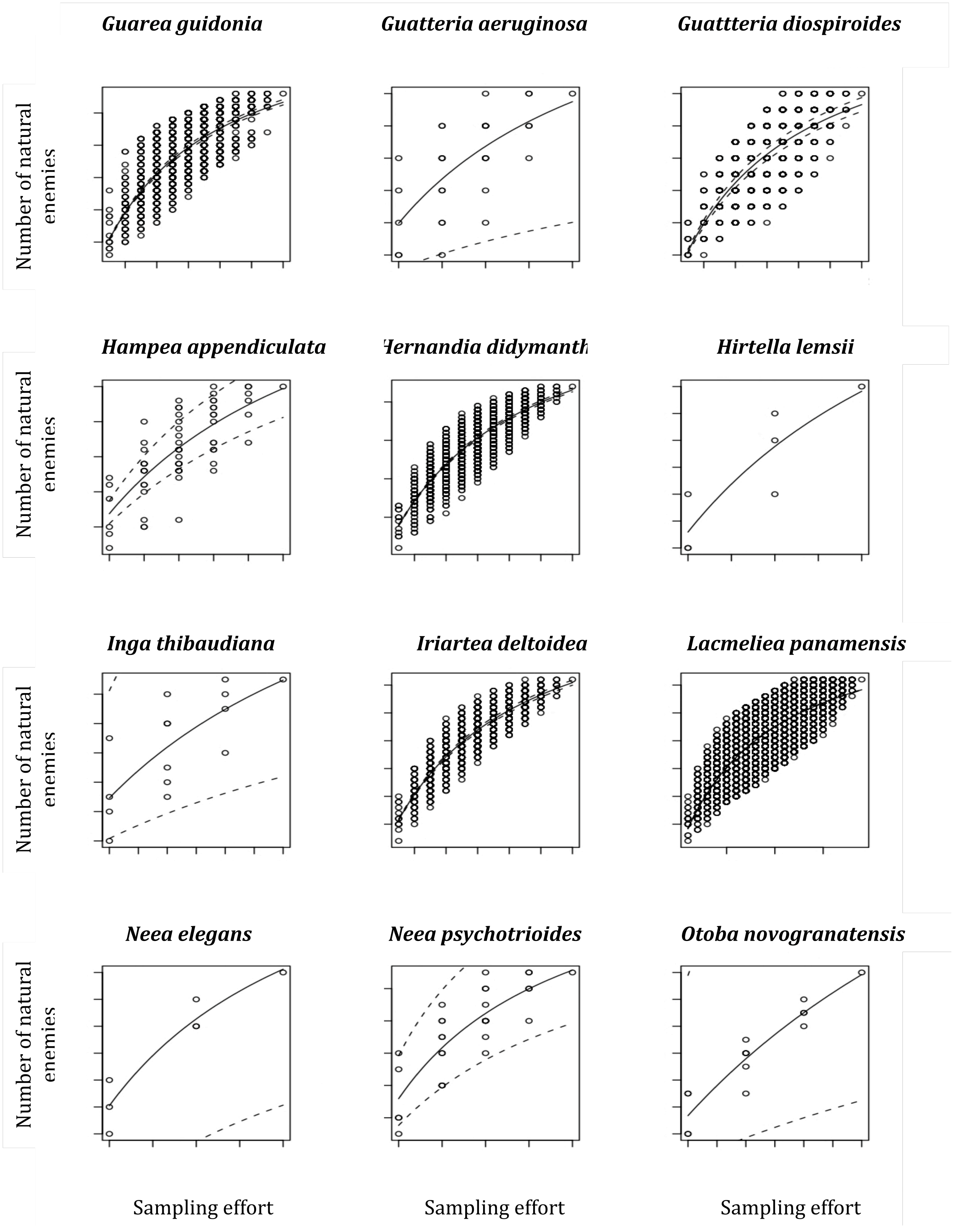


Figure A.3. (cont’d)

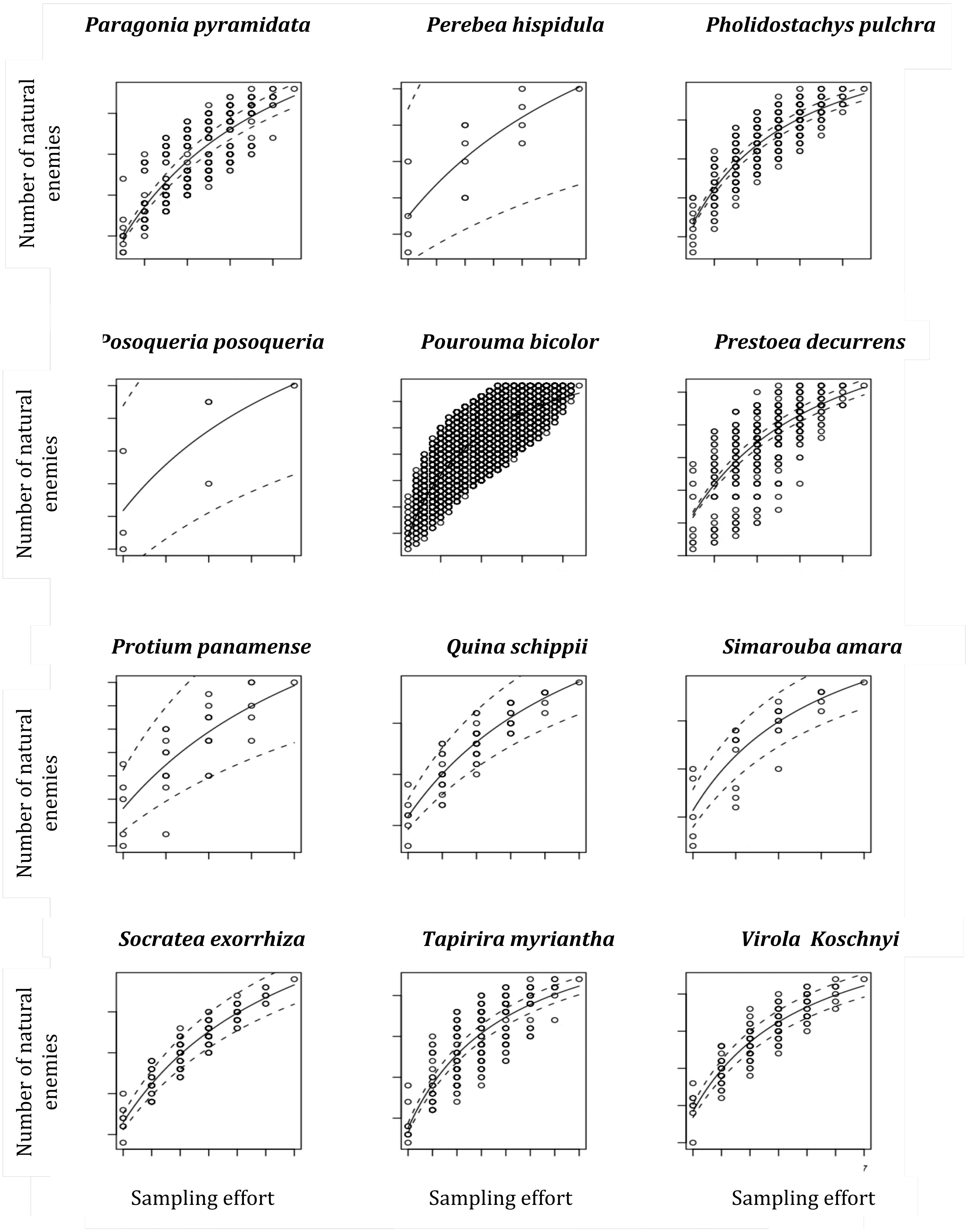
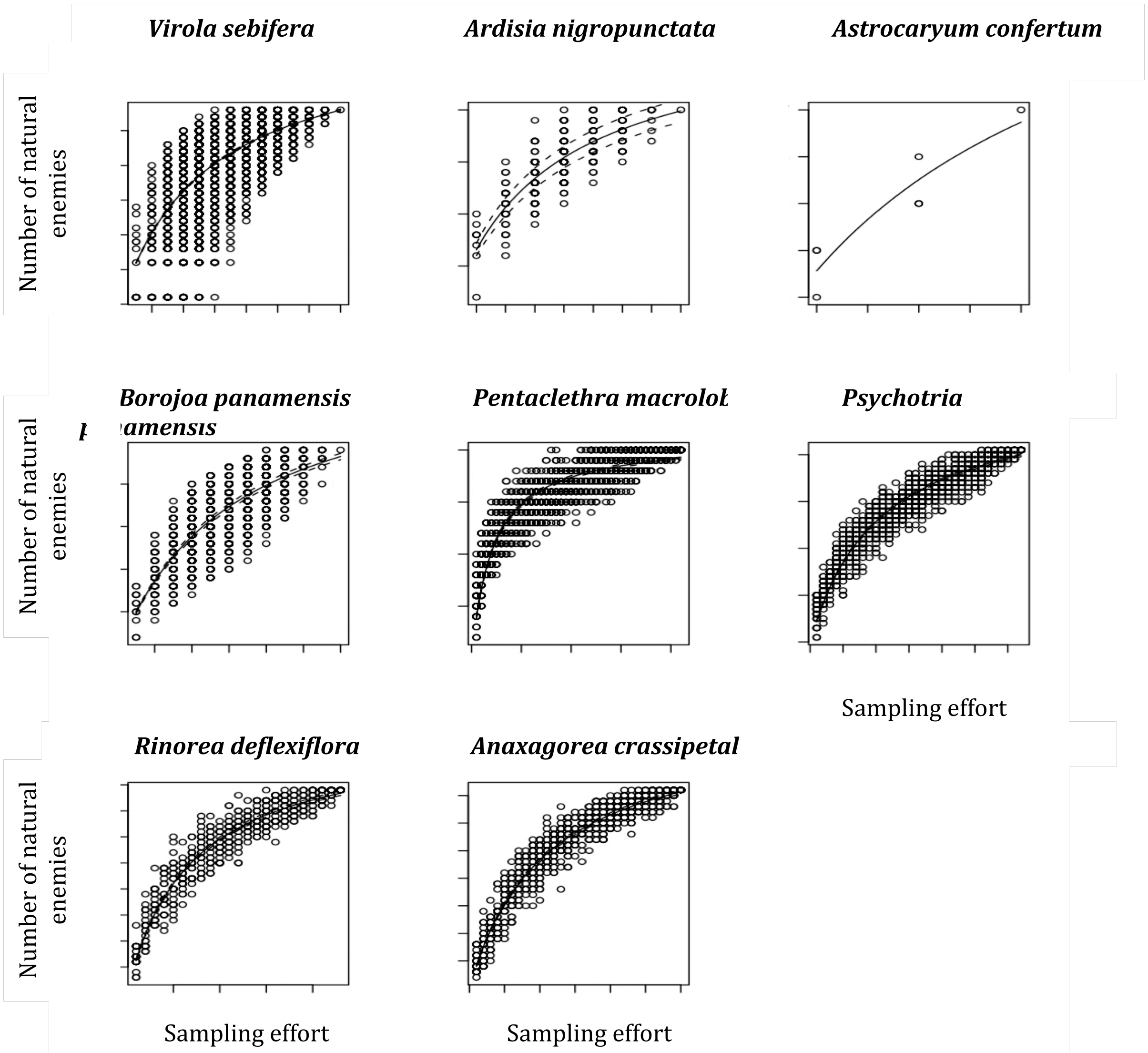


Figure A.3. (cont'd)



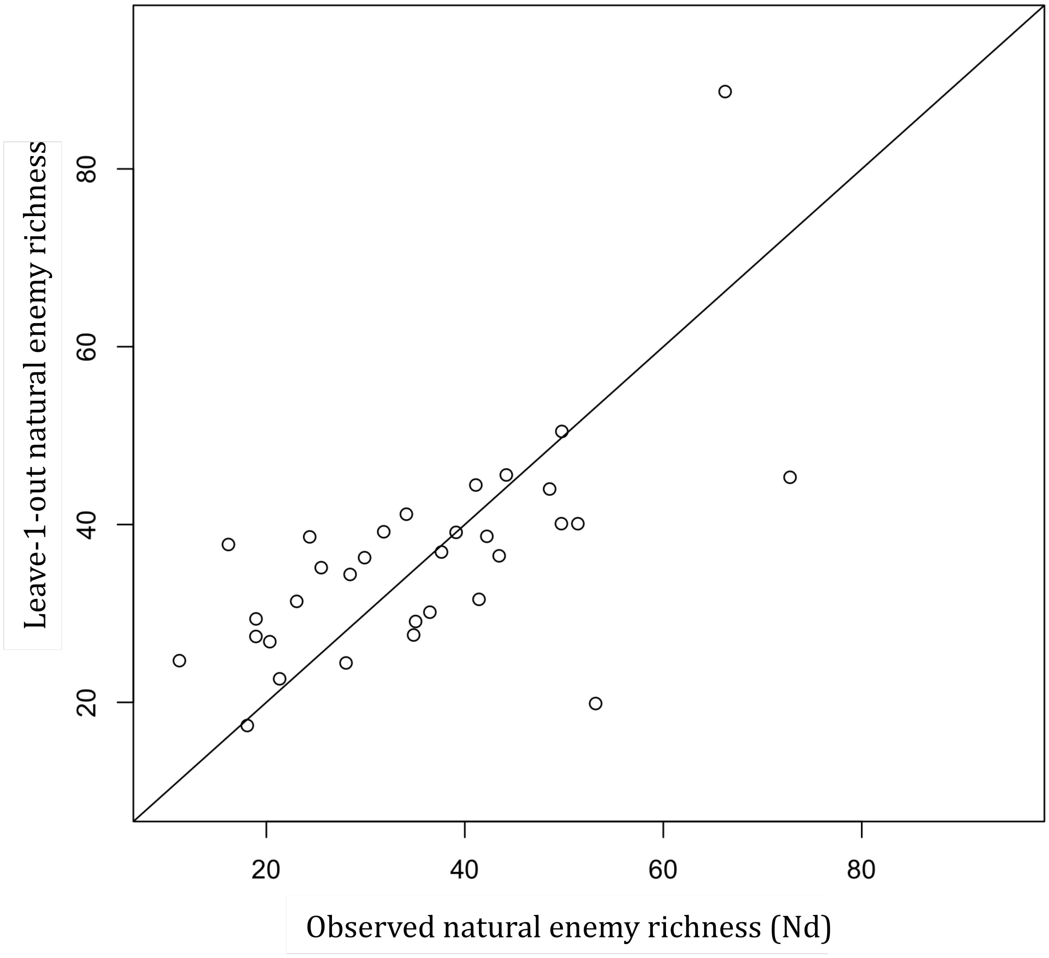


Figure A.4. Observed maximum of natural enemies hosted by species versus predicted maximum number of natural enemies from leave-one-out. The line represents the y=x

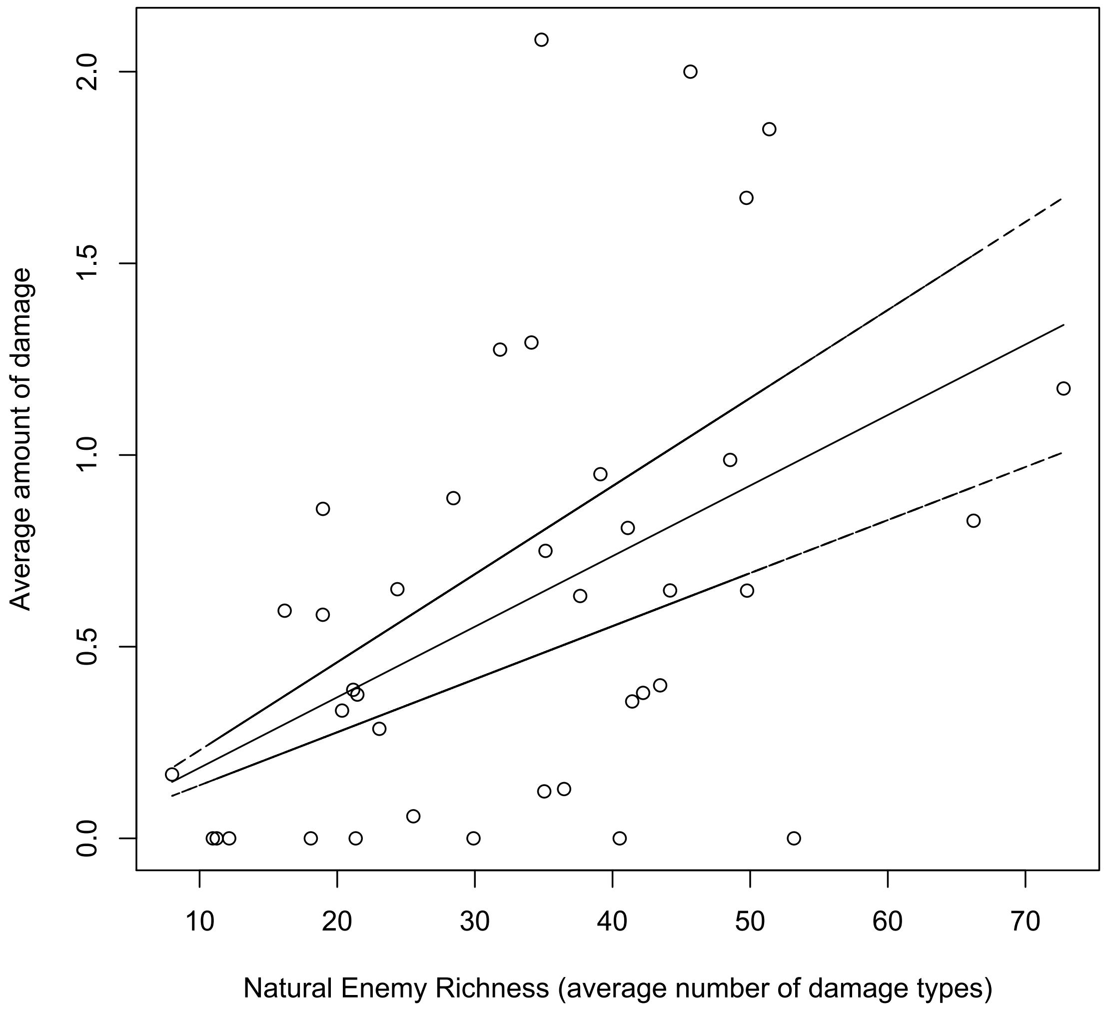


Figure A.5th. Natural enemy richness is positively correlated to the amount of damage. The thicker lines represent the confidence intervals.

APPENDIX B

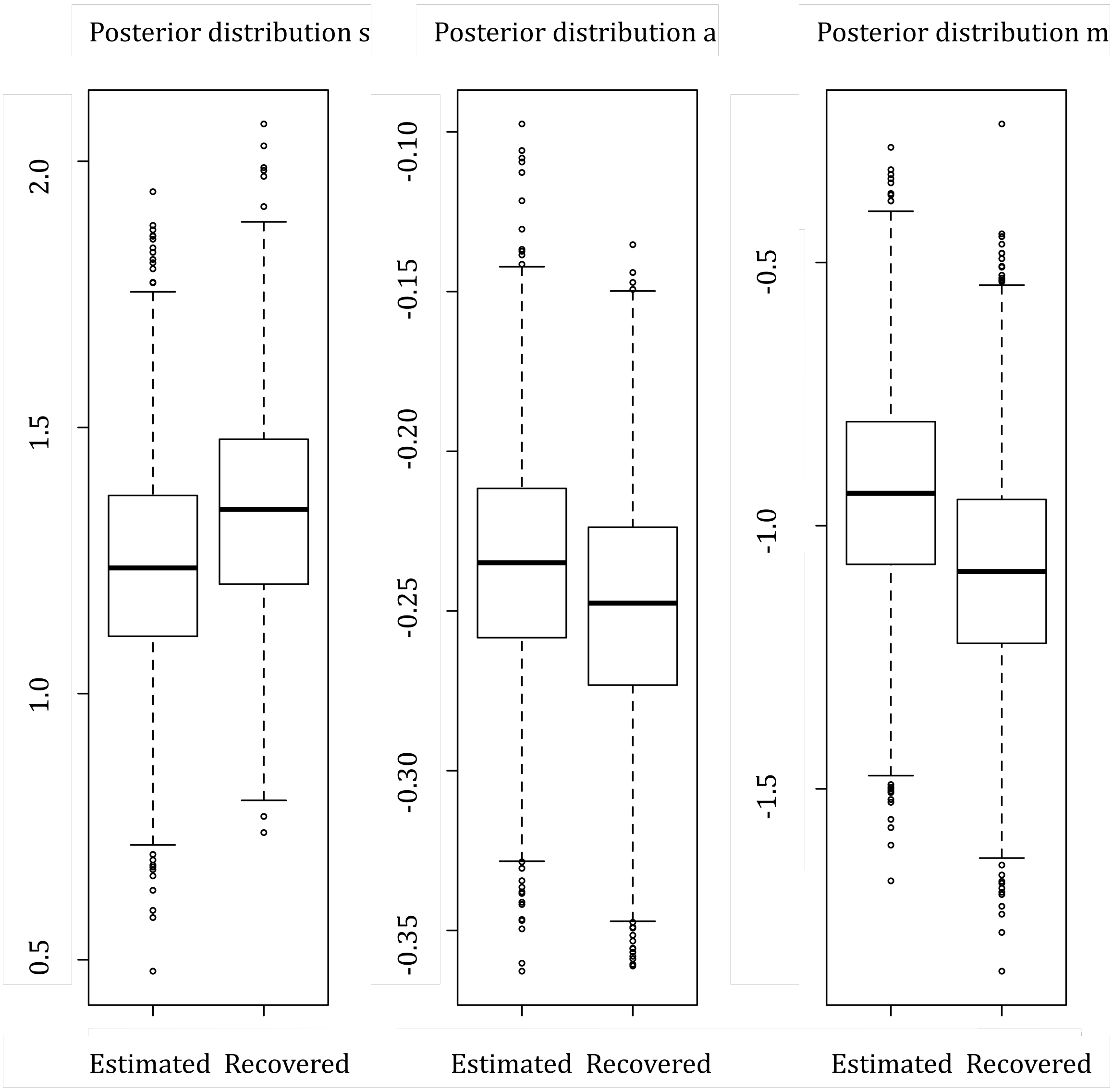


Figure B.1. Estimated and recovered posterior distributions for the damage/mortality model (Model 1).

APPENDIX C

Table C.1. Table of the p-value of paired t-test realized between species composition of two 1-year time periods. 0: 2000, 1:2001 ,..., 9:2009. Among the tests only two showed a significance difference in species composition, they are in red. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

	0	1	2	3	4	5	6	7	8	9
0		0.1360	0.1702	0.4657	0.4493	0.4220	0.7922	0.7128	0.4169	0.2414
1			0.2194	0.5765	0.5593	0.3392	0.6498	0.8383	0.753	0.355
2				0.06195	0.03375	0.1081	0.05	0.1738	0.1518	0.8627
3					0.9173	0.9757	0.7474	0.9994	0.4442	0.1517
4						0.8513	0.7642	0.966	0.5133	0.1408
5							0.8525	0.9886	0.5511	0.2229
6								0.8113	0.2333	0.06721
7									0.3573	0.1930
8										0.1813
9										

Table C.2. Table of the p.value of paired t-test realized between species composition of two 2-year time periods.

	2000-2001	2002-2003	2004-2005	2006-2007	2008-2009
2000-2001		0.3227	0.6139	0.9157	0.3824
2002-2003			0.2701	0.3109	0.5736
2004-2005				0.9048	0.3388
2006-2007					0.06966
2008-2009					

Table C.3. Table of the p.value of paired t-test realized between species composition of two 5-year time periods.

	2005-2009
2000-2004	0.7123

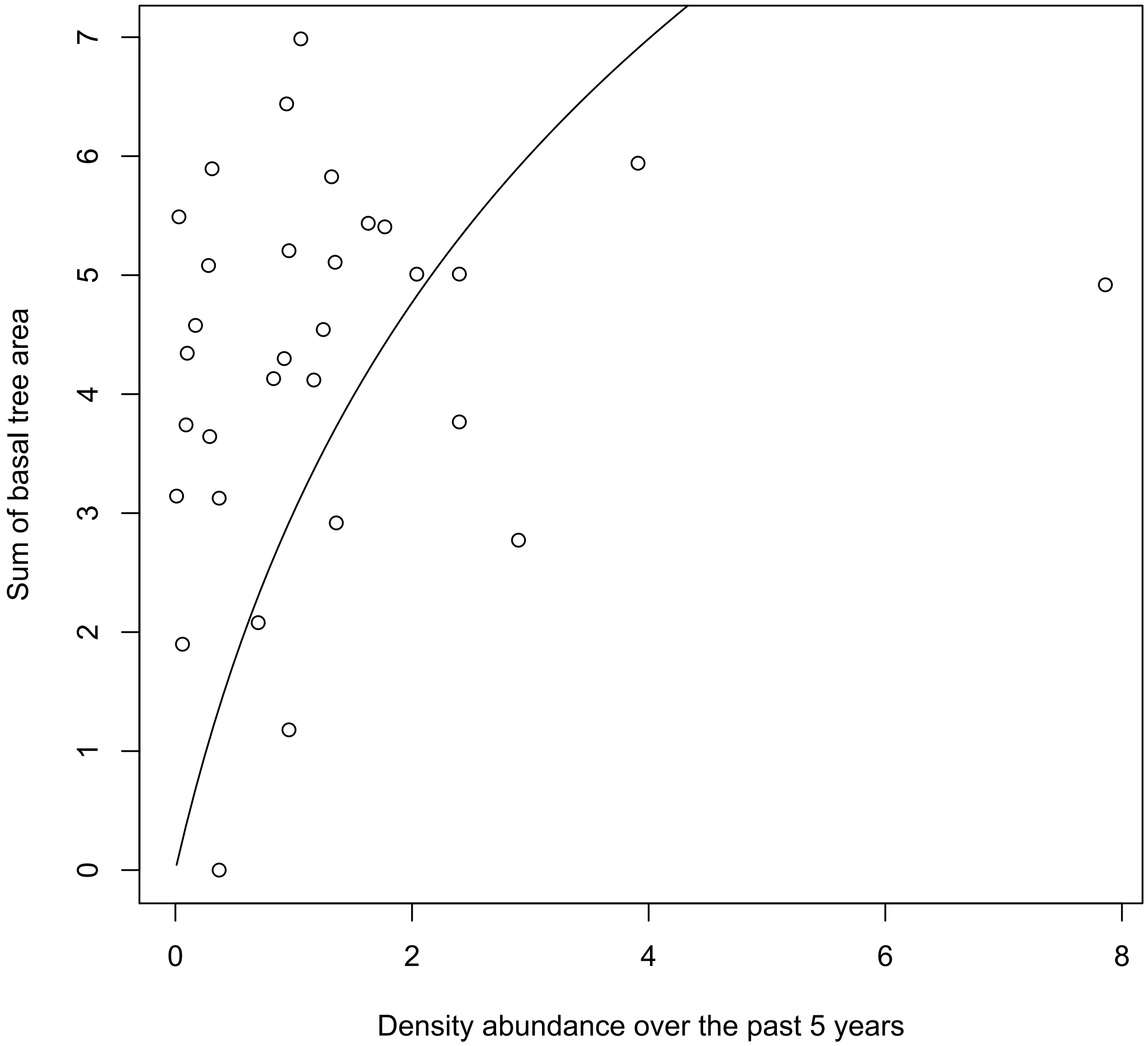


Figure C.1. Relation between species abundance at the tree level (log(sum of basal tree area + 1)), and at the seedling level (Abunndance over the past 5 years).

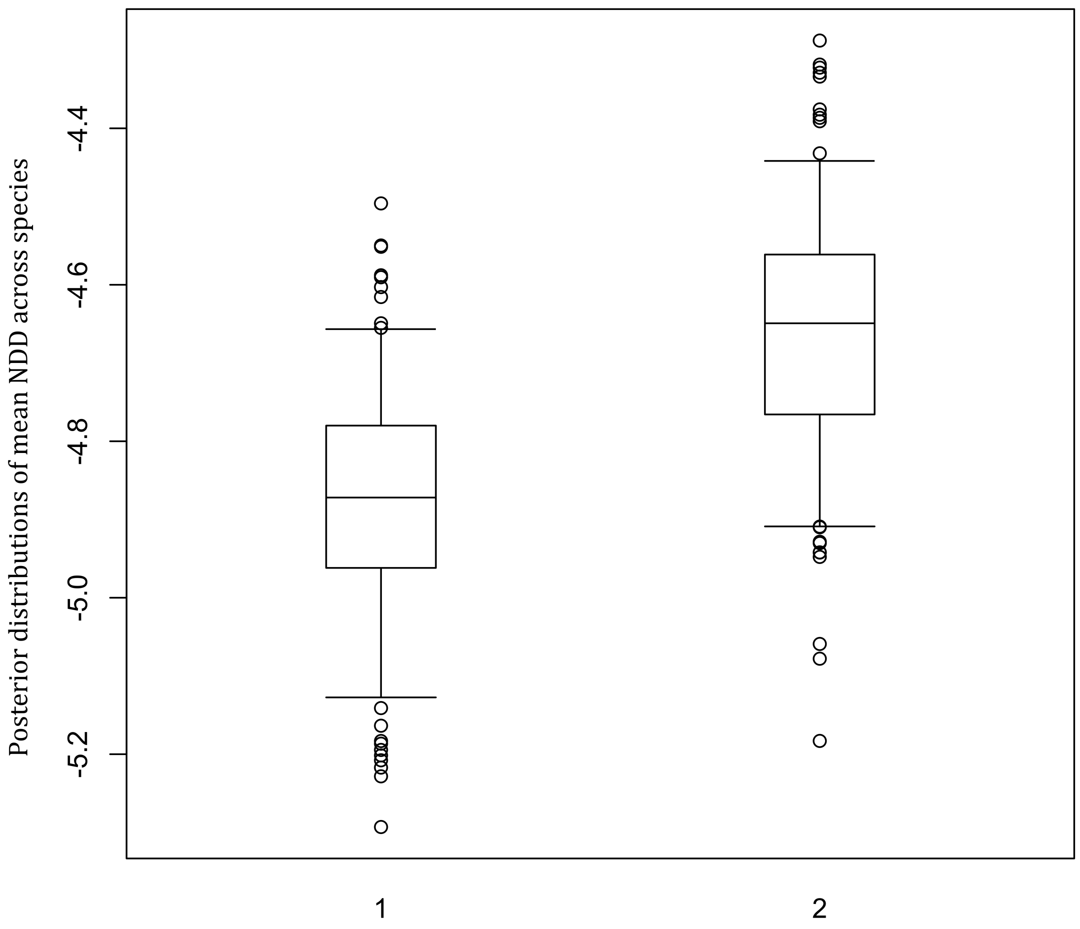


Figure C.2. Posterior distributions of the mean NDD across species at the 5-years interval (1: from 2000 to 2004, 2: from 2005 to 2009). The wiskers extend to the credible intervals.

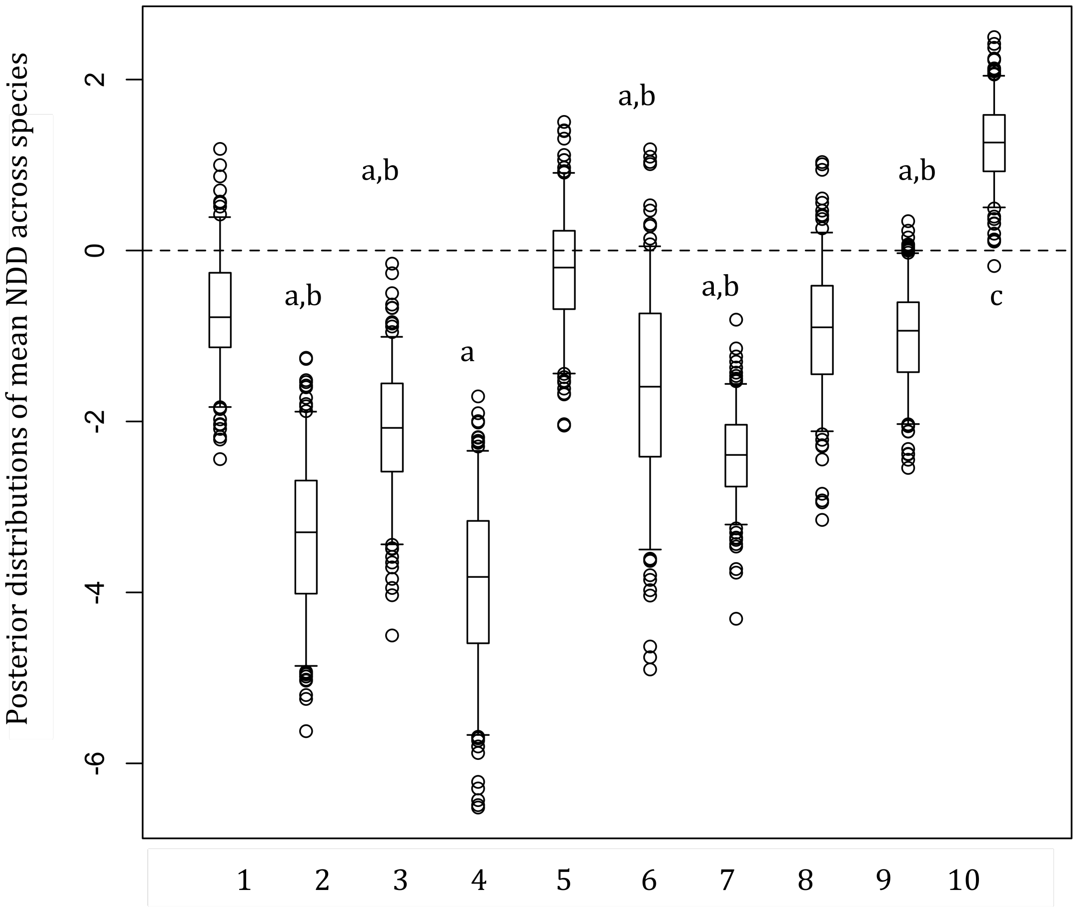
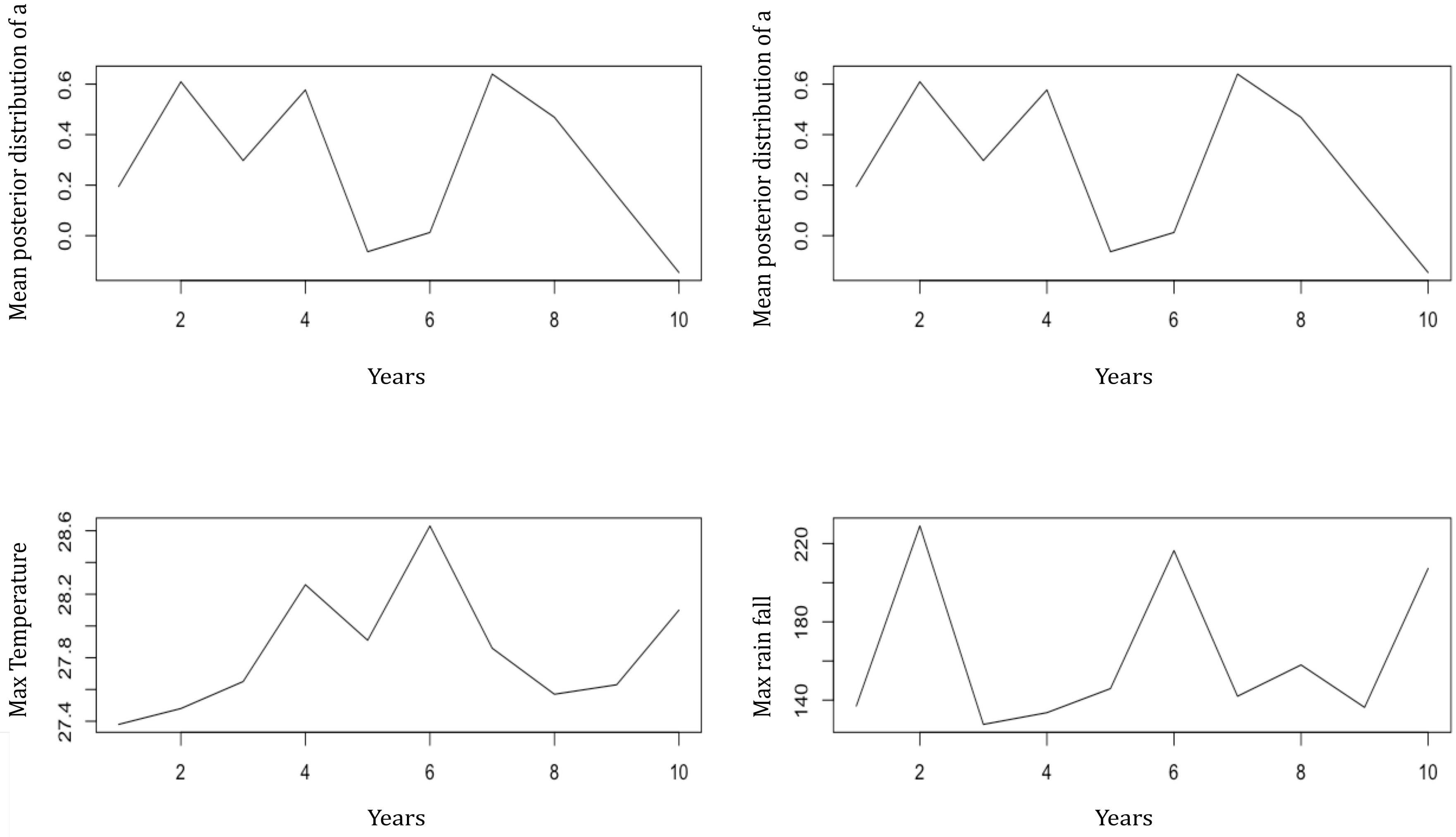


Figure C.3. Posterior distribution of the mean NDD across species over each 1-year interval. 1: 2000, 2: 2001, 3: 2002, ..., 10: 2009. Wiskers expend to the credible intervals. Letters show where the distributions are significantly different from each other.

Figure C.4. Fluctuations of the mean posterior distribution of a (effect of species abundance on NDD), in relation to fluctuations of climate variables across years (Maximum temperature and Maximum rain fall).



APPENDIX D

$$\begin{cases} x_i(k+1) & = x_i(k)exp\left[b_i(k) - BNDD(x_i(k))x_i(k) - c(k)y(k)\right], \quad i = 1, 2, \cdots, n \\ y(k+1) & = y(k)exp\left[\sum_{i=1}^{n} d_i(k)x_i(k) - e(k)y(k) - r(k)\right], \\ BNDD(x_i(k)) & = x_i(k)^2 - x_i(k)\alpha(k), \quad i = 1, 2, \cdots, n \end{cases} \tag{1.3}$$

The system is permanent

Lemma 1 *If it exists $l_0 \in \mathbb{N}$ such as $x_i(l_0) \leq x_i(l_0+1)$, then:*

$$\forall k \geq l_0, \ x_i(k) \leq p_i, \quad i = 1, 2, \cdots, n$$

with $p_i = R_i \ \exp\left[b_i^u + (4/27)\alpha^{u,3}(k)\right]$, where R_i is a root of a polynome depending on α^u and b_i^u.

Proof:

•First prove that:

$$\exists j_0 \in \mathbb{N} \quad x_i(j_0) \leq x_i(j_0+1) \quad \Longrightarrow \quad x_i(j_0+1) \leq p_i, \quad i = 1, 2, \cdots, n$$

From (1.3) we have:

$$0 \leq b_i(j_0) - BNDD(x_i(j_0))x_i(j_0) - c(j_0)y(j_0)$$

$$0 \leq b_i(j_0) - x_i(j_0)^3 + x_i(j_0)^2\alpha(j_0) - c(j_0)y(j_0)$$

$$0 \leq b_i(j_0) - x_i(j_0)^3 + x_i(j_0)^2\alpha(j_0)$$

$$0 \leq b_i^u - x_i(j_0)^3 + x_i(j_0)^2\alpha^u$$

Let's call Q_i the polynome

$$Q_i(x) = b_i^u - x^3 + x^2\alpha^u$$

Then

$$delta_i = -4\alpha^{u,3}b_i^u - 27(b_i^u)^2 \leq 0$$

So it exists one unique real solution R_i such as

$$Q_i(R_i) = 0$$

It can be shown that $R_i \geq \frac{2\alpha}{u,3}$. R_i depends only on α^u and b_i^u.
Further analyses of Q_i show that

$$0 \leq Q_i(x) => x \leq R_i$$

Moreover Q_i is maximal for $x = \frac{2\alpha^u}{3}$.
So

$$x_i(j_0) \leq R_i$$

$$x_i(j_0+1) \leq R_i \exp\left[Q_i(\frac{2\alpha^u}{3})\right] = R_i \exp\left[b_i^u + (4/27)\alpha^{u,3}\right] \overset{def}{=} p_i$$

•Now we will prove the lemma by contradiction.
So let's assume that it exists $l_0 \in \mathbb{N}$ such as $x_i(l_0) \leq x_i(l_0+1)$, and that

$$\exists w_0 \in \mathbb{N}, w_0 \gneq l_0 \quad / x_i(w_0) \gneq p_i$$

Let's call $\tilde{w}_0$ the smallest integer such as $x_i(\tilde{w}_0) \gneq p_i$. Then

$$\tilde{w}_0 \geq l_0 + 2$$

$$x_i(\tilde{w}_0 - 1) \leq p_i < x_i(\tilde{w}_0)$$

Thus

$$x_i(\tilde{w}_0 - 1) \leq x_i(\tilde{w}_0)$$

We deduce from the first part of the proof: $x_i(\tilde{w}_0) \leq p_i$.

By contradiction

$$\forall k \geq l_0,\ x_i(k) \leq p_i, \quad i = 1, 2, \cdots, n$$

Theorem 1 *For every solution* $(x_1(k), \cdots, x_n(k), y(k))$ *of system (1.3), it exists* $k_1 \in \mathbb{N}$ *such that:*

$$\forall k \geq k_1 \quad x_i(k) \leq p_i, \quad i = 1, 2, \cdots, n \tag{1}$$

$$\forall k \geq k_1 \quad y(k) \leq q \tag{2}$$

where p_i *are constant depending on* α^u *and* b_i^u*, and* q *is a constant depending on* $\alpha^u, b_i^u, r^l, e^l, d_i^u$.

Proof: •The previous lemma proves the first result when it exists $l_0 \in \mathbb{N}$ such as $x_i(l_0) \leq x_i(l_0+1)$. In this case $k_1 = l_0$.
Now we assume that such an integer l_0 doesn't exist. It means that $x_i(k+1) < x_i(k)$ for all $k \in \mathbb{N}$. As $(x_i(k))_k$ is bounded under by 0, it admits a limit. Let's call that limit $\bar{x}_i$.
By taking the limit in the ith equation of system (1.3), we get

$$\lim_{k \to +\infty} \Big(b_i(k) - BNDD(x_i(k))x_i(k) - c(k)y(k) \Big) = 0$$

Moreover

$$b_i(k) - NDD(x_i(k))x_i(k) - c(k)y(k) \leq Q_i(x_i(k))$$

So

$$0 \leq Q_i(\bar{x}_i)$$

So we conclude that $\bar{x}_i \leq R_i$. Note that $R_i < p_i$. This leads to the existence of $k_1 \in \mathbb{N}$ such that $\forall k \geq k_1 \quad x_i(k) \leq p_i$. This complete the proof of (1).

•According to (1) there exists an integer k_1 such that: $x_i(k) \leq p_i$, $\forall k \geq k_1$. By using the system we get for $k \geq k_1$

$$y(k+1) \leq y(k) \exp\left[\sum_{i=1}^{n} d_i^u p_i - r^l - e^l y(k)\right] = \frac{\exp\left[\sum_{i=1}^{n} d_i^u p_i - r^l\right]}{e^l} e^l y(k) \exp\left[-e^l y(k)\right]$$

Moreover

$$e^l y(k) \exp\left[-e^l y(k)\right] \leq 1$$

So we conclude that $(y(k))_k$ is bounded above, and we have:

$$\exists k_1 \in \mathbb{N} \quad \forall k \geq k_1 \quad y(k) \leq \frac{\sum_{i=1}^{n} d_i^u(p_i) - r^l}{e^l} \overset{def}{=} q$$

Lemma 2 *We assume that*

$$b_i^l - c^u q > 0 \tag{H1}$$

If it exists an integer $l_0 \geq k_1$ such as $x_i(l_0) \geq x_i(l_0+1)$, then:

$$\forall k \geq l_0 \quad x_i(k) \geq \tilde{s}_i, \quad i = 1, 2, \cdots, n$$

with $\tilde{s}_i \overset{def}{=} r_i exp\left[b_i^l - p_i^3 + p_i^2\alpha^l - c^u q\right]$. Where r_i is a root of a polynome depending on α^l, b_i^l, c^u, q.

Proof:

•First prove that there exists constants $\tilde{s}_i$ such that:

$$\exists j_0 \geq k_1 \quad x_i(j_0) \geq x_i(j_0+1) \quad \Longrightarrow \quad x_i(j_0+1) \geq \tilde{s}_i, \quad i = 1, 2, \cdots, n$$

We assume it exists $j_0 \geq k_1$ such as

$$x_i(j_0+1) \leq x_i(j_0)$$

then from (1.3) we have

$$b_i(j_0) - BNDD(x_i(j_0))x_i(j_0) - c(j_0)y(j_0) \leq 0$$

And from Theorem 1:

$$b_i^l - x_i(j_0)^3 + x_i(j_0)^2\alpha^l - c^u q \leq 0$$

Let's call M_i the polynome

$$M_i(x) = b_i^l - x^3 + x^2\alpha^l - c^u q$$

Then

$$delta_i = -4\alpha^{l,3} b_i^l - 27(b_i^l - c^u q)^2$$

Thanks to (H1) we have: $delta_i < 0$. So it exists one unique real solution r_i such as

$$M_i(r_i) = 0$$

r_i depends only on α^l, c^u, q. It can also be shown that $r_i \geq \frac{2\alpha^l}{3}$. Further analyses of M_i show that $M_i(x) \leq 0 \Rightarrow x \geq r_i$, and that M_i is decreasing for $x \geq r_i$.
So $x_i(j_0) \geq r_i$. Moreover we know that $x_i(j_0) \leq p_i$. If $p_i < r_i$ we conclude that j_0 doesn't exist. Otherwise we conclude that

$$x_i(j_0+1) \geq r_i exp\left[M_i(p_i)\right] \overset{def}{=} \tilde{s}_i, \quad i = 1, 2, \cdots, n$$

•Now we will prove the lemma by contradiction.
So let's assume that it exists $l_0 \in \mathbb{N}$ such as $x_i(l_0) \geq x_i(l_0+1)$, and that it exists $w \gneq l_0 + 1$ such that $x_i(w) \lneq \tilde{s}_i$.
Let's call w_0 the smallest w such as $x_i(w_0) \lneq \tilde{s}_i$.
Then

$$w_0 \geq l_0 + 2$$

$$x_i(w_0) \leq \tilde{s}_i \leq x_i(w_0 - 1)$$

Thus

$$x_i(w_0) \leq x_i(w_0 - 1)$$

We deduce from the first part of the proof: $x_i(w_0) \geq \tilde{s}_i, \quad i = 1, 2, \cdots, n$.
The lemma is proved by contradiction.

Theorem 2 *We assume that*

$$b_i^l - c^u q > 0 \tag{H1}$$

For every solution $(x_1(k), \cdots, x_n(k), y(k))$ of system (1.3), it exists $k_2 \in \mathbb{N}$ such that:

$$\forall k \geq k_2 \quad x_i(k) \geq \tilde{p}_i, \quad i = 1, 2, \cdots, n \tag{3}$$

$$\forall k \geq k_2 \quad y(k) \geq \tilde{q} \tag{4}$$

where $\tilde{p}_i$ and $\tilde{q}$ are constant depending on b_i^l, α^l, c^u, α^u, b_i^u, e^l, d_i^l.

Proof: •The previous lemma proves the first result when it exists $l_0 \in \mathbb{N}$ such as $x_i(l_0) \geq x_i(l_0+1)$.
Now we assume that $x_i(k+1) > x_i(k)$ for all $k \in \mathbb{N}$. As $(x_k)_k$ is bounded above, it admits a limit. Let's call that limit $\underline{x}_i$.

By taking the limit in the ith equation of system (1.3), we get

$$\lim_{k\to+\infty}\Big(b_i(k) - BNDD(x_i(k))x_i(k) - c(k)y(k)\Big) = 0$$

Moreover for large enough $k \in \mathbb{N}$

$$b_i(k) - NDD(x_i(k))x_i(k) - c(k)y(k) \geq b_i^l - x_i(k)^3 + x_i(k)^2\alpha^l - c^u q = M_i(x_i(k))$$

Leading to

$$M_i(\underline{x}_i) \leq 0$$

So, thanks to the lemma, we have: $\underline{x}_i \geq r_i$.
As $r_i \leq p_i$ we know that $M_i(p_i) \leq 0$. So $r_i \geq r_i exp\left[M_i(p_i)\right] = \tilde{s}_i$. So there exists $k_2 \in \mathbb{N}$ such that $\forall k \geq k_2 \quad x_i(k) \geq \frac{1}{2}\tilde{s}_i \overset{def}{=} \tilde{p}_i$. This complete the proof of (3).

•In a first time let's assume there exists $l_0 \in \mathbb{N}$ such that $y(l_0) \geq y(l_0+1)$. Then:

$$y(l_0) \geq y(l_0+1) \geq y(l_0)\exp\left[\sum_{i=1}^{n} d_i^l(\tilde{p}_i) - r^u - e^u y(l_0)\right]$$

So, $\sum_{i=1}^{n} d_i^l(\tilde{p}_i) - r^u - e^u y(l_0) \leq 0$, leading to:

$$y(l_0) \geq \frac{\sum_{i=1}^{n} d_i^l(\tilde{p}_i) - r^u}{e^u} \overset{def}{=} \tilde{q}$$

If such an integer l_0 doesn't exist, this means that $\left(y(k)\right)_k$ is increasing. As it is bounded above, it admits a limit denoted by $\bar{y}$. By taking the limit in the (n+i)th equation of system (1.3), we get:

$$\lim_{k\to+\infty}\left(\sum_{i=1}^{n} d_i(k)x_i(k) - e(k)y(k) - r(k)\right) = 0$$

In particular there exists $k_2 \in \mathbb{N}$ such that

$$\forall k \geq k_2 \quad \sum_{i=1}^{n} d_i(k)x_i(k) - e(k)y(k) - r(k) \leq 1$$

So

$$\forall k \geq k_2 \quad \sum_{i=1}^{n} d_i^l(\tilde{p}_i) - r^u \leq \sum_{i=1}^{n} d_i(k)x_i(k) - r(k) \leq e(k)y(k) \leq e^u y(k)$$

$$\forall k \geq k_2 \quad \tilde{q} \leq y(k)$$

The proof of (4) is achieved.

Theorem 3 *Stable positive equilibrium*

Let's two positive solutions of the system be

$$(x_1, \cdots, x_n, y) \quad and \quad (\widehat{x}_i, \cdots, \widehat{x}_n, \widehat{y})$$

such that

$$b_i^l - c^u q > 0 \tag{H1}$$

$$\max\left(1 + 3p_i^3\left(\frac{p_i}{\tilde{p}_i}\right)^3 + 2\alpha^u p_i^2\left(\frac{p_i}{\tilde{p}_i}\right)^2, c^u q\frac{q}{\tilde{q}}\right) < 1 \tag{H2}$$

$$\left|1 - e^l\tilde{q}\left(\frac{\tilde{q}}{q}\right)\right| + \sum_{i=1}^{n} d_i^u p_i\left(\frac{p_i}{\tilde{p}_i}\right) < 1 \tag{H3}$$

Then we claim that

$$\lim_{k\to+\infty}\big(y(k) - \widehat{y}(k)\big) = 0$$
$$\lim_{k\to+\infty}\big(x_i(k) - \widehat{x_i}(k)\big) = 0, \quad i = 1, 2, \cdots, n$$

Proof: Let

$$x_i(k) = \widehat{x}_i(k)\exp(u_i(k))$$
$$y(k) = \widehat{y}(k)\exp(v(k))$$

Then we have

$$x_i(k+1) = \widehat{x}_i(k+1)\exp(u_i(k+1))$$
$$exp(u_i(k+1)) = \frac{x_i(k+1)}{\widehat{x}_i(k+1)}$$

From system (1.3)

$$\exp(u_i(k+1)) = \frac{x_i(k)\exp(b_i(k) - x_i(k)^3 + x_i(k)^2\alpha - c(k)y(k))}{\widehat{x}_i(k)\exp(b_i(k) - \widehat{x}_i(k)^3 + \widehat{x}_i(k)^2\alpha - c(k)\widehat{y}(k))}$$

$$= \frac{\widehat{x}_i(k)\exp(u_i(k))\exp(b_i(k) - \widehat{x}_i(k)^3\exp(3u_i(k)) + \alpha\widehat{x}_i(k)^2\exp(2u_i(k)) - c(k)\widehat{y}(k)\exp(v(k)))}{\widehat{x}_i(k)\exp(b_i(k) - \widehat{x}_i(k)^3 + \widehat{x}_i(k)^2\alpha - c(k)\widehat{y}(k))}$$

$$= \exp(u_i(k) - \widehat{x}_i(k)^3(\exp(3u_i(k)) - 1) + \alpha\widehat{x}_i(k)^2(\exp(2u_i(k)) - 1) - c(k)\widehat{y}(k)(\exp(v(k)) - 1))$$

So

$$u_i(k+1) = u_i(k) - \widehat{x}_i(k)^3(\exp(3u_i(k)) - 1) + \alpha\widehat{x}_i(k)^2(\exp(2u_i(k)) - 1) - c(k)\widehat{y}(k)(\exp(v(k)) - 1)$$

We demonstrate in the same way that

$$v(k+1) = v(k) + \sum_{i=1}^{n} d_i(k)\widehat{x}_i(k)(\exp(u_i(k)) - 1) - e(k)\widehat{y}(k)(\exp(v(k)) - 1)$$

According to a Taylor's formula, there exist $\theta_{i,1}$, $\theta_{i,2}$, θ in $]0, 1[$ such that
$\exp(3u_i(k)) - 1 = 3u_i(k)\exp(3\theta_{i,1}u_i(k))$,
$\exp(2u_i(k)) - 1 = 2u_i(k)\exp(2\theta_{i,2}u_i(k))$, and $\exp(v(k)) - 1 = v(k)\exp(\theta v(k))$. This implies:

$$u_i(k+1) =$$
$$u_i(k)\left(1-3\widehat{x}_i(k)^3\exp(3\theta_{i,1}u_i(k))+2\alpha(k)\widehat{x}_i(k)^2\exp(2\theta_{i,2}u_i(k))\right)-c(k)v(k)\widehat{y}(k)\exp(\theta v(k))$$
$$v(k+1)=v(k)\left[1-e(k)\widehat{y}\exp(\theta v(k))\right]+\sum_{i=1}^{n} d_i(k)\widehat{x}_i(k)u_i(k)\exp(\theta_i u_i)$$

So

$$\begin{aligned}|u_i(k+1)| &\leq | u_i(k)|(1+3p_i^3\left(\frac{p_i}{\tilde{p_i}}\right)^3+2\alpha^u p_i^2\left(\frac{p_i}{\tilde{p_i}}\right)^2)+c^u|v(k)|q\frac{q}{\tilde{q}}\\ &\leq \left(\max\left[1+3p_i^3\left(\frac{p_i}{\tilde{p_i}}\right)^3+2\alpha^u p_i^2\left(\frac{p_i}{\tilde{p_i}}\right)^2, c^u q\frac{q}{\tilde{q}}\right]\right)\max(|v(k)|,|u_1(k)|,\cdots,|u_n(k)|)\end{aligned}$$

And for v:

$$\begin{aligned}|v(k+1)| &\leq |v(k)||1-e^l\tilde{q}\left(\frac{\tilde{q}}{q}\right)|+\sum_{i=1}^{n} d_i^u p_i|u_i(k)|\left(\frac{p_i}{\tilde{p_i}}\right)\\ &\leq \left(\left|1-e^l\tilde{q}\left(\frac{\tilde{q}}{q}\right)\right|+\sum_{i=1}^{n} d_i^u p_i\left(\frac{p_i}{\tilde{p_i}}\right)\right)\max(|v(k)|,|u_1(k)|,\cdots,|u_n(k)|)\end{aligned}$$

Let's call and assume

$$\begin{aligned}\lambda_i &= \max\left[1+3p_i^3\left(\frac{p_i}{\tilde{p_i}}\right)^3+2\alpha^u p_i^2\left(\frac{p_i}{\tilde{p_i}}\right)^2, c^u q\frac{q}{\tilde{q}}\right] < 1\\ \delta &= \left|1-e^l\tilde{q}\left(\frac{\tilde{q}}{q}\right)\right|+\sum_{i=1}^{n} d_i^u p_i\left(\frac{p_i}{\tilde{p_i}}\right) < 1\end{aligned}$$

Let's call $\zeta = max(\lambda_i,\delta)$. We have $\zeta < 1$. Then we get

$$max(|u_i(k+1)|,|v(k+1)|) \leq \zeta max(|u_i(k)|,|v(k)|)$$

So for $k* \lneq k$

$$max(|u_i(k)|,|v(k)|) \leq \zeta^{k-k*} max(|u_i(k*)|,|v(k*)|)$$

Then by taking the limit we get: $\lim_{k\to+\infty} max(|u_i(k)|,|v(k)|)=0$.
So

$$\begin{aligned}&\lim_{k\to+\infty} u_i(k)=0, \quad i=1,2,\cdots,n\\ &\lim_{k\to+\infty} v(k)=0\end{aligned}$$

Which leads to

$$\begin{aligned}&\lim_{k\to+\infty}(y(k)-\widehat{y}(k))=0\\ &\lim_{k\to+\infty}(x_i(k)-\widehat{x_i}(k))=0, \quad i=1,2,\cdots,n\end{aligned}$$

The positive solution of the system is stable.

There is a stable positive periodic solution

There exists a positive integer ω that is a common multiple of the period of all coefficients of system (1.3).

Let's notice $D^{n+1} = [\tilde{p}_1, p_1] \times \cdots \times [\tilde{p}_n, p_n] \times [\tilde{q}, q]$.

We consider the application ϕ that maps an initial state $(x_1(0), \cdots, x_n(0), y(0)) \in D^{n+1}$ to the solution of system (1.3) at generation ω.

From theorem 1 and theorem 2, we demonstrated that the set D^{n+1} is an invariant set of system (1.3). So ϕ maps the compact set D^{n+1} to itself. Therefore, according to the Brouwer fixed point theorem, we know that the continuous application ϕ has a fixed point.

Moreover the solution of (1.3) passing through this fixed point is periodic.

From the theorem 3, we know that this positive periodic solution is stable. Therefore we demonstrated that our system (1.3) has one stable positive periodic solution.