

**The Relationship between Species Diversity and
Ecosystem Function in Low- and High-diversity
Tropical African Forests**

Kelvin Seh-Hwi Peh

Submitted in accordance with the requirements for the degree of
Doctor of Philosophy

The University of Leeds
School of Geography

July, 2009

The candidate confirms that the work submitted is his/her own and that appropriate credit has been given where reference has been made to the work of others. This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

Acknowledgements

The forest plots for long-term monitoring at the Dja Faunal Reserve used in this research were established by Dr. Simon Lewis and Dr. Bonaventure Sonké. I would like to thank my supervisors Dr. Simon Lewis and Professor Jon Lloyd for all their guidance and support during my time at Leeds. Many thanks also go to Professor Bonaventure Sonké for his support while I was in Cameroon. Financial support by Marie Curie EST Fellowship is gratefully acknowledged.

I would like to thank my mother, Pang Ah Sa, and Dr. Jonathan Eyal for helping me with the preparation of field materials, and also for their never-ending support. I am grateful to Dr. Jean-Michel Onana (National Herbarium of Cameroon), Dr. Guillaume Dzikouk (Birdlife Cameroon), Sheila Hannan (Kenya Airways), Gabriella Contini (Swiss International Airlines) and Jeanette Sonké for their logistic support. Many people have also offered assistance and advice during my Ph.D.; my thanks go to Professor Oliver Phillips, Dr. Tim Baker, Dr. Bill Kunin, Dr. Stephen Cornell, Dr. Carlos Quesada, Dr. Andy Turner, Dr. Kuo-Jung Chao, Dr. Ted Feldpausch, Dr. Olivier Hardy, Dr. Jennifer Powers, Lindsay Banin, Franziska Schrodt, Olivier Séné, and the Ecology and Global Change group within the School of Geography. Dr. Carlos Quesada, Hermann Taedoung, Lindsay Banin, Marie-Noël Djuikouo Kamdem, Nguembou Kamgang Charlemagne and Olivier Séné assisted me in my field work. Dr. Quesada also helped with the soil sampling and advised on the laboratory soil analyses of this project.

All support staff were always generous with their assistance; my gratitude goes to laboratory staff Rachel Gasior, David Ashley, John Corr, Miles Ratcliffe and Martin Gilpin. Finally, I would like to thank the community at Somalomo, especially Alaman Sikiro and Moïse Mikame, for their field assistance and good company, and for making my long stays at the Dja Faunal Reserve comfortable and enjoyable.

Abstract

Species diversity may affect ecosystem functions, such as the productivity of a system or the stability of that production. Understanding these relationships is important if the impacts of biodiversity loss are to be predicted, and management of ecosystems to be altered to maintain essential ecological processes.

Three randomly chosen pairs of long-term forest monitoring plots in moist evergreen tropical forest of the Dja Faunal Reserve, south-eastern Cameroon, were used in this study. One of each pair contained a naturally-occurring low-diversity of species dominated by *Gilbertiodendron dewevrei*, (monodominant forest) and the second contained a high diversity of species (mixed forest). All trees with the diameter at breast height (dbh) ≥ 10 cm were measured, and litterfall traps were set up in these plots. The monodominant forest plots had higher basal area and above-ground biomass (AGB). Leaf production in the Dja mixed forest was greater than that reported from any other tropical forest in the world, and I speculate that this may be due to the disturbance caused by megaherbivores. However, AGB growth (coarse wood production), litterfall (leaf, woody litter, reproductive structures and fine wood) productivity and above-ground net primary productivity (ANPP) were not significantly different. There were no significant differences in physical and chemical soil properties between the pairs of the two forest types. Taxon sampling curves confirm that the monodominant forests have lower species richness, species density and population density than the mixed forests, in terms of trees with dbh of ≥ 10 cm. After controlling for phylogeny, the three most important determinants of the likelihood of successful establishment of non-dominant species in the monodominant *Gilbertiodendron* forests were the relative abundance in adjacent mixed forests, wood density and light requirement for seedling establishment.

Within the mixed forest plots, there were significant positive relationships between biomass productivity (in terms of AGB growth, litterfall productivity and ANPP) and tree species diversity. However, the productivity-diversity relationship with the monodominant forest plots showed no clear trends. This suggests that while diversity is positively related to various measures of productivity, the impact of individual species, in this case, *G. dewevrei*, can be the dominant impact in some situations.

Temporal variability of the litterfall productivity decreased with diversity within the monodominant forest. However, increasing diversity had no effect on the stability of litterfall productivity within the mixed forest. This suggests that increasing diversity increases the stability of production, but this effect saturates at the level of diversity found in mixed forests.

Using experimental leaf litter addition, the estimated rate of decomposition of leaf litter in the mixed forest was faster than that of the monodominant forest, and was influenced by the tree diversity. *Gilbertiodendron* leaves did breakdown faster when mixed with a 'standard' control leaves after three months, but this mixing-effect was not observed after five months onwards. This suggests that diversity effects can be short-lived. The higher quality control leaves did not breakdown faster when mixed with *Gilbertiodendron* leaves. This shows that diversity effects can be context-dependent.

These findings show the complexity of the relationship of tree species diversity on aspects of tropical forest productivity and the stability of that production.

Contents

Acknowledgements	ii
Abstract	iii
Content	iv
Figures	vii
Tables	ix
Abbreviations	x
Chapter 1. Introduction	1
1.1. Project rationale.....	1
1.2. Species diversity and ecosystem function	2
1.3. Monodominance in tropical lowland forests	6
1.3.1. Diversity of monodominance in tropical lowland forests	10
1.3.2. Explaining classical monodominance	16
1.3.3. Linking the hypotheses: a new framework	22
1.4. Thesis synopsis	25
1.5. Thesis aims and objectives	26
Chapter 2. Soil properties of low-diversity monodominant forests and adjacent high-diversity mixed forests in south-eastern Cameroon	28
2.1. Introduction	28
2.2. Methods	30
2.2.1. Study area	30
2.2.2. Plot establishment	34
2.2.3. Soil sampling.	34
2.3. Results and Discussion	37
2.4. Summary	46
Chapter 3. Tree diversity of monodominant forest in relation to its adjacent mixed forest	47
3.1. Introduction	47
3.2. Methods	49
3.2.1. Tree sampling	49
3.2.2. Tree species traits	50
3.2.3. Species richness estimations	51
3.2.4. Statistical analyses of establishment	52
3.3. Results	54
3.3.1. Comparing monodominant and mixed forest diversity	54
3.3.2. Life-history traits	56

3.4. Discussion	66
3.5. Summary	71
Chapter 4. Above-ground tree growth and fine litter productivity in relation to tree species diversity	73
4.1. Introduction.	73
4.2. Methods	75
4.2.1. Tree measurement	75
4.2.2. Estimations of AGB growth.	77
4.2.3. Estimations of litter productivity and ANPP	80
4.2.4. Statistical analyses	81
4.3. Results	84
4.3.1. Basal area	84
4.3.2. Above-ground biomass	89
4.3.3. Diversity and above-ground biomass growth.....	94
4.3.4. Litterfall productivity and ANPP	98
4.3.5. AGB growth of <i>Gilbertiodendron dewevrei</i>	110
4.4. Discussion	114
4.5. Summary	118
Chapter 5. Litterfall phenological observations: biomass allocation and variability in litterfall productivity in two lowland forests with contrasting tree diversity... 120	120
5.1. Introduction	120
5.2. Methods	122
5.2.1. Tree survey and litterfall collection	123
5.2.2. Data analyses on biomass allocation and temporal patterns of litterfall	124
5.2.3. Data analyses on diversity effects	126
5.3. Results	130
5.3.1. Total litterfall and biomass allocation	130
5.3.2. Phenological patterns and climatic variables	135
5.3.3. Effects of diversity	138
5.4. Discussion	142
5.5. Summary	145
Chapter 6. Effects of tree species diversity on leaf litter decomposition	146
6.1. Introduction	146
6.2. Methods	148
6.2.1. Litterfall observations	149
6.2.2. Litterbag experiments	150

6.3. Results	152
6.3.1. Observations in two forest types	152
6.3.2. Mixed-litter decomposition experiments	155
6.4. Discussion	159
6.4.1. Observational evidence on diversity impacts on decomposition	159
6.4.2. Experimental evidence on effects of litter mixture	161
6.4.3. Limitations	164
6.5. Summary	165
Chapter 7. Conclusion	166
7.1. Research synthesis	166
7.2. Conservation implications	174
7.3. Recommendations of future work	177
References	182
Appendix A	207
Appendix B	212

Figures

Figure 1.1 Types of monodominance in tropical lowland forests.....	11
Figure 1.2 Model of positive feedbacks leading to monodominance	24
Figure 2.1 Map of study location	31
Figure 2.2 Monthly rainfall and temperature patterns based on average of 30 years data ..	32
Figure 2.3 Soil properties–clay, silt and sand	39
Figure 2.4 Soil properties–median particle size, pH and bulk density	40
Figure 2.5 Soil properties–C, N and C/N ratio	41
Figure 2.6 Soil properties–concentrations of labile P, inorganic P and total P.....	42
Figure 2.7 Soil properties–concentrations of Al, Ca, K, Mg and Na.....	43
Figure 2.8 Soil properties–concentrations of Ba, Cu, Fe, Mn, Ni, Si and Zn	44
Figure 3.1 Allocation of stem number and proportion of stem number in dbh classes.....	55
Figure 3.2 Number of species, species density and population density	58
Figure 3.3 Association of wood density and successful establishment	61
Figure 3.4 Principal component of ordination of tree species.....	63
Figure 4.1 Regressions of tree height on tree diameter at breast height	79
Figure 4.2 AGB growth vs. species diversity index and species number	83
Figure 4.3 AGB and basal area estimations of study plots	86
Figure 4.4 Basal area growth of study plots	87
Figure 4.5 Basal area net change of study plots	88
Figure 4.6 AGB of study plots	90
Figure 4.7 AGB growth of study plots	91
Figure 4.8 AGB net change of study plots	93
Figure 4.9 AGB growth vs. species diversity in monodominant forest	95
Figure 4.10 AGB growth vs. species diversity in mixed forest	96
Figure 4.11 Litterfall productivity of study plots	99
Figure 4.12 Litterfall mass vs. tree species diversity in monodominant forest	100
Figure 4.13 Litterfall mass vs. trap species number in monodominant forest	101
Figure 4.14 Litterfall mass vs. species diversity in mixed forest	102
Figure 4.15 Litterfall mass vs. trap species number in mixed forest	103
Figure 4.16 ANPP of study plots.....	105
Figure 4.17 ANPP vs. species diversity in monodominant forest	106
Figure 4.18 ANPP vs. trap species number in monodominant forest	107
Figure 4.19 ANPP vs. species diversity in mixed forest	108
Figure 4.20 ANPP vs. trap species number in mixed forest	109
Figure 4.21 Growth rates of species with maximum dbh ≤ 50 cm	111

Figure 4.22 Growth rates of species with maximum dbh between 50 and 100 cm	112
Figure 4.23 Growth rates of species with maximum dbh ≥ 100 cm	113
Figure 5.1 Monthly rainfall and temperature patterns in 2007–2008	125
Figure 5.2 Quadrat species number vs. trap species number	127
Figure 5.3 Simpson's diversity index vs. trap species number	128
Figure 5.4 Litterfall mass of each litter category	132
Figure 5.5 Absolute amounts of litterfall of each litter category	133
Figure 5.6 Relative amounts of litterfall of each litter category	134
Figure 5.7 Litterfall patterns of each litter category	136
Figure 5.8 Standard deviation vs. trap species number	139
Figure 5.9 Standard deviation vs. species diversity	140
Figure 6.1 Leaf litter/standing crop vs. Simpson's diversity index	154
Figure 6.2 Litter mass loss vs. time	156
Figure 6.3 Decomposition rates vs. species diversity	158
Figure 7.1 Proportion of lianas in study plots	171
Figure 7.2 Mortality rate in study plots	178

Tables

Table 1.1 Diversity of monodominant species in tropical forests.....	8
Table 2.1 Soil physical and chemical properties	38
Table 3.1 Non-parametric species richness estimations	57
Table 3.2 Importance of traits for establishment in monodominant forest.....	60
Table 3.3 Binary regression models for establishment success.....	64
Table 3.4 Final multiple logistic regression model for establishment success.....	65
Table 4.1 Details of study plots	76
Table 4.2 Statistics for diversity effects on biomass productivity	97
Table 5.1 Statistics for collection date and site effects on litterfall mass....	137
Table 5.2 Statistics for climatic variables on litterfall mass.....	137
Table 6.1 Decomposition rates of bay and <i>Gilbertiodendron</i> litter.....	157
Table 7.1 Summary of the effects of species diversity on the ecosystem functions	167

Abbreviations

AGB	Above-ground biomass
AIC	Akaike's Information Criteria
Al	Aluminium
ANPP	Above-ground net primary productivity
B	Boron
Ba	Barium
C	Carbon
Ca	Calcium
Co	Cobalt
Cr	Chromium
Cu	Copper
CEC	Cation exchange capacity
CV	Coefficient of variation
dbh	Diameter at breast height
EM	Ectomycorrhizal
Fe	Iron
GLM	General linear model
K	Potassium
LSD	Least-Significant Difference
Mg	Magnesium
Mn	Manganese
Mo	Mollybdenum
N	Nitrogen
Na	Sodium
Ni	Nickel
P	Phosphorous
PCA	Principal component analysis
S	Sulphur
SD	Standard deviation
Se	Selenium
Si	Silicon
Sr	Strontium
Ti	Titanium
V	Vanadium
Zn	Zinc

1. Introduction

1.1. Project rationale

Degradations of biological resources by human disturbance often make the headlines of newspapers. Such interest is often based on the following ecological rationale: A reduction of biological diversity will negatively affect vital ecosystem functions that regulate the Earth system upon which humans ultimately depend. Under the United Nations Earth Summit in Rio de Janeiro in 1992, which was reinforced in Johannesburg in 2002, one of the key reasons for conserving biological diversity is that it promotes human well-being by providing with the conditions and processes that sustain and fulfil human lives, i.e. ecosystem services (Convention on Biological Diversity, <http://www.biodiv.org>). Therefore, a key question for our century is: how do we manage biological resources to reduce biodiversity loss and maintain their essential ecological processes for sustained use. This requires a scientific understanding of the relationships between the numbers and identities of the species in ecosystems and the functioning of these systems. Better understanding of these relationships in tropical forests is the core aim of this thesis.

There is substantial evidence showing that biological diversity influences various ecosystem functions (see Section 1.2). However, little work has been done to validate the strength and form of the relationship between biological diversity and various ecosystem functions in tropical forest ecosystems, despite tropical forests playing a critical role in many Earth system processes (see Section 1.2). In this project, empirical studies were undertaken to elucidate the effects of tree species diversity on ecological processes in natural tropical forests. Field work involving plot-based monitoring of tropical forest trees was undertaken in naturally-occurring forest dominated by *Gilbertiodendron dewevrei* (monodominant forest) and naturally-occurring adjacent high-diversity forest, to improve our understanding of the effects of tree species diversity on various critical tropical forest functions such as above-ground biomass (AGB) production (equivalent to coarse wood production), litterfall productivity (equivalent to

leaf, woody litter, reproductive structures and fine wood production), above-ground net primary productivity (ANPP; the sum of AGB growth and litterfall productivity), temporal variability of litterfall mass and leaf litter decomposition rate in African tropical forest. I chose to focus my study in African forests because we have the least knowledge about African forest ecology compared to those in South-east Asia and Amazon (Lewis *et al.* 2009).

This chapter will introduce two key themes of the thesis, namely (1) the relationship between diversity and function (Section 1.2), and (2) the phenomenon of low-diversity or monodominant tropical forests, where higher diversity forests would be expected (Section 1.3). Based on reviews of relevant literature, this introduction will clarify some theory and concepts regarding diversity-functioning relationship and monodominance in tropical forests.

1.2. Species diversity and ecosystem function

The relationship between native species diversity and ecosystem functioning has attracted attention not only because it has potentially important consequences for conservation, but also because of interest in understanding the relative importance of processes that contribute to various ecosystem functions such as productivity.

In early experimental studies, many authors believed that some ecosystem functions emerging from a species assemblage could be improved by increasing the number of species that led to a more complete utilization of the total resource spectrum (e.g., Tilman 1999a). Therefore, such complementarity in resource use, through niche differentiation and facilitation, may result in greater productivity in a more species-rich system than the one that consisted of only single species (Tilman 1999b). Although described simply as a linear relationship in most of these studies, another school of researchers argued that the relationship between species diversity and function is more complex than this implies (Loreau *et al.* 2002). One reason to prevent drawing an early conclusion on the shape of this diversity-functioning relationship is that most of these early experimental studies assembled communities at random from species pool. Although random sampling depicts a possible scenario of random gradual loss of

diversity, whereby disturbance or change in abiotic conditions become too extreme for the species' survival (Loreau *et al.* 2001), it could potentially introduce a mechanism that includes dominant, functionally important species with increasing diversity (sampling effects) and leads to an increase in average primary production (Loreau *et al.* 2001). Hence, in such a case, the ecosystem function improved with increasing diversity, caused by the presence of more productive species, rather than by better use of resources through the niche complementarity of different species.

Recent evidence suggests that underlying mechanisms, sampling effects and complementarity, occur and are not mutually exclusive. For example, a more diverse synthetic grassland community was shown to include both dominant species and a particular combination of species that are complementary (Tilman *et al.* 2001). Similarly, diversity-mediated effects on biomass accumulation, nutrient retention and primary productivity have been shown to remain significant after controlling for the strong effects of certain dominant species (Hooper *et al.* 2005). Furthermore, complementarity has been shown to occur when combinations of species belonged to different functional groups (Loreau & Hector 2001). However, the significance of complementarity within an assemblage can also be affected by compositional effects (Duarte *et al.* 2006), biotic influences (Thébaud & Loreau 2005) and abiotic environmental conditions (Hooper *et al.* 2005).

In addition, we can define different levels of diversity and identify their relative importance on functioning. While 'species diversity' considers species richness in terms of numbers of species as separate entities, 'functional group diversity' considers species composition where species with similar effects on a specific ecosystem-level process (i.e., functional traits) are clustered together as functional groups (Hooper *et al.* 2005). These different levels of diversity can independently influence ecosystem functioning. The effects of different diversity level are shown clearly in the Cedar Creek Natural History Area grassland experiments in Minnesota (Reich *et al.* 2004). This study showed that species and functional diversity independently influence biomass accumulation in response to elevated atmospheric carbon dioxide concentration and nitrogen deposition. Curiously, both species and functional

richness effects were not dependent on specific species, functional groups or function group combinations, even though several studies have shown that the effects of functional richness tend to outstrip those of species richness (e.g., Petchey 2004). Therefore, the potential mechanism behind the positive effects of diversity on functions was complementarity (Reich *et al.* 2004).

There is some evidence that many ecosystem processes are more stable with increasing diversity (biological insurance). Stability in these studies is measured as persistence, resistance, recovery, predictability, spatial variability and temporal variability in aggregated community properties in the presence of disturbance or environmental changes (Ives & Carpenter 2007). The results from earlier experiments, however, were plagued by several confounding factors. For example, the species diversity variation in earlier studies often resulted from a fertilization gradient and fertilization itself may have an impact (for details, see Huston 1997). Fortunately, the link between diversity and stability shown by the recent studies that avoided those pitfalls is clear: increasing diversity of species or functional groups has been observed to enhance the stability of biomass production, soil carbon accumulation, resistance to invasion, persistence of plant communities, and ecosystem recovery (Hooper *et al.* 2005). Potential mechanisms that affect the stability of an ecosystem function in response to changing species or functional diversity can be compensatory interactions as observed in Mongolian grassland under varying climatic conditions (Bai *et al.* 2004); or facilitative interactions as observed in bryophyte communities under drought conditions (Mulder *et al.* 2001). However, evidence for the mechanisms underlying stability responses is still scarce and remains under investigation (Hooper *et al.* 2005).

Despite a growing collection of studies on the effects of diversity on function, there is a surprisingly limited range of systems being investigated. These studied systems can be divided into aquatic or terrestrial communities. Some of the most interesting mathematical models of diversity and functioning relationships have come from aquatic systems. For example, the first study from a whole-systemic perspective on an ecosystem with multi-trophic structure was the theoretical work by Aoki & Mizushima (2001) who quantitatively included the diversity of the

whole trophic structure of natural aquatic systems; as predicted by biological insurance theory, the increased diversity resulted in greater whole-system stability. However, the question is how well these mathematical models based on aquatic systems pertain to terrestrial species conservation. Likewise, are the models based on aquatic systems applicable to terrestrial species? Several assumptions, such as the lack of partitioning of resources, that were built into models might not necessarily reflect the reality in many natural systems (Cottingham *et al.* 2001) and more studies are needed to confirm these underlying assumptions for specific cases (for assumptions on diversity-stability theory, see Chapter 5).

Aquatic micro- and mesocosm experiments have contributed enormously to our ability to test for the diversity-function relationship. Because of their size and short generation time, microbial communities enable studies at larger spatial and temporal scales and provide function patterns that are consequences of varying species richness across different scales of experimental habitat patches and over many generations. In addition, the microbial communities or mesocosm can be grown rapidly to maximum densities and their species composition is determined by the system dynamics *per se*. Therefore, this removes the confounding factors of initial condition, such as densities and relative species abundance, on functioning established in terrestrial experimental communities. However, the applicability of the results from these studies in natural systems remains unclear. The unrealistic spatio-temporal conditions in these overly-simplified systems might not translate well to larger real-world spatial scales; and we might not be able to extrapolate their results to the species of interest to conservation. Hence, a potentially fruitful approach is to use more natural systems, which have more direct relevance to conservation, to test the generality of the diversity-functioning relationship derived from micro- and mesocosm experiments.

The most-studied terrestrial system is the grassland, where evidence suggests that increasing diversity enhances biomass production. Also, now we know that the temporal variability of various processes in grassland decreases with increasing diversity. However, can we extrapolate our understanding from better studied system to the others? The answer is probably “no”. This is because functioning responses to diversity could saturate at different

species richness in different systems. For example, nutrient retention and nutrient use efficiency of an ecosystem comprising herbaceous species maximized at higher species richness than that of longer-lived perennials (Hooper *et al.* 2005). Moreover, we have limited knowledge about extinction processes in different ecosystems triggered by habitat destruction, invasion of alien species, environmental pollution, climate change and human over-harvesting. The patterns observed under a particular scenario of species extinction may vary among different natural systems (Cardinale *et al.* 2000). Conversely, diversity-function relationship seen for a particular ecosystem may be different under a changed scenario of species loss. Careful observational and experimental studies that factor in the realistic extinction process, trophic structure and spatio-temporal scale may increase our understanding and allow generalisations across ecosystems that are of direct relevance to conservation.

In summary, while experimental studies are able to control for many confounding effects on diversity-functioning relationship, observational studies in a natural ecosystems are able to incorporate features such as non-random species assemblage and multi-trophic influence that are rarely reflected in experimental study designs. These ‘natural’ experiments have been conducted in systems such as Mediterranean forests (Vilà *et al.* 2007), temperate forests (Caspersen & Pacala 2001) and tropical tree plantations (Erskine *et al.* 2006), and have provided evidence of a positive association between species richness and wood production at the regional scale. However, few studies have been conducted in tropical forests. One example is a meta-analysis by Phillips *et al.* (1994) showing that there was a link between tropical forest dynamic and tree species richness. In another study by Bunker *et al.* 2005, a simulation of 18 possible extinction scenarios using the data from a 50 ha tropical forest plot shows that carbon storage in tropical forest depends on species composition. In this study, I utilized the natural gradients in tropical forest ecosystem within monodominant and mixed forests to explore these diversity-functioning relationships. My direct observational approach is complementary to the earlier stimulation and meta-analytical studies.

1.3. Monodominance in tropical lowland forests

Tropical lowland forest is rich in plant diversity not only at the regional scale, but also within single localities (Hubbell 2004). However, contrary to the popular belief that tropical forests are always associated with high alpha-diversity, there are large areas of tropical forest dominated by only one species in terms of the proportion of the total canopy trees present. Early literature recorded many examples of monodominance in forests in all the major tropical regions of the world (Table 1.1). Although the dominant species may account for >80 % of total canopy trees in many of these monodominant forests (Hart *et al.* 1989), the common definition of monodominance is with at least 60 % of canopy-level trees belong to the same species (Torti *et al.* 2001).

Monodominance in tropical lowland forests has aroused interest amongst tropical ecologists because understanding the diversity and distribution of species is a major goal in ecology. Van Zon (1915) first noted the occurrence of monodominance of *Dryobalanops aromatica* that does not conform to the typical species-rich scenario of a tropical lowland forest, and highlighted the phenomenon that monodominant forests often occur adjacent to mixed species-rich forests. Hart *et al.* (1989) and Connell & Lowman (1989) were among the first researchers to speculate on the causes of the co-occurrence of these two distinct forest types. Hart *et al.* (1989) hypothesized that monodominant forests are the result of the lack of large-scale disturbances over long periods. Connell & Lowman (1989) showed that canopy tree diversity decreases with increasing dominance of one canopy species within their study plots, but overall species composition in terms of number of species within monodominant forests remains the same over large areas as compared to their adjacent mixed counterparts. According to this work, the monodominant forest could be the result of an ectomycorrhizal (EM) association of dominant tree species, with the association conferring various advantages, such as greater ability to secure nutrients and greater protection from pathogens, which may then give rise to monodominance.

Table 1.1 Diversity of monodominant species in tropical lowland forest. Seed mass is the average oven-dried weight unless * denotes average fresh weight, ** average air-dried weight and n.a. data not available. Seed mass data was retrieved at Liu *et al.* (2008) except *Gilbertiodendron dewevrei* which I obtained the average air-dried weight from 12 seeds collected at the Dja Faunal Reserve, Cameroon. This list is not exhaustive.

Type	Distribution	Family	Name	Seed weight (g)	Reference
Classical	Central Africa	Burseraceae	<i>Aucoumea klaineana</i> Pierre	0.01	Maisels 2004
	Central Africa	Fabaceae	<i>Cynometra alexandri</i> C.H.Wright	n.a.	Hart et al. 1989
	Central Africa	Fabaceae	<i>Gilbertiodendron dewevrei</i> (De Wild.) J.Léonard	20.40**	Conway 1992
	Central Africa	Fabaceae	<i>Talbotiella gentii</i> Hutchinson & Greenway	n.a.	Richards 1996
	Central Africa	Fabaceae	<i>Tetraberlinia tubmaniana</i> J.Léonard	n.a.	Connell & Lowman 1989
	Malesia	Dipterocarpaceae	<i>Dryobalanops aromatica</i> C.F.Gaertn.	3.75**	Ithoh 1995
	Malesia	Dipterocarpaceae	<i>Parashorea malaanonan</i> Merr.	1.89	Richards 1996
	Malesia	Dipterocarpaceae	<i>Shorea curtisii</i> Dyer ex King	n.a.	Grubb et al. 1994
	Malesia	Lauraceae	<i>Eusideroxylon zwageri</i> Teijsm. & Binn.	28.57**	Richard 1996
	Neotropics	Apocynaceae	<i>Aspidosperma excelsum</i> Benth.	n.a.	Richards 1996
	Neotropics	Burseraceae	<i>Dacryodes excelsa</i> Vahl	n.a.	Richards 1996
	Neotropics	Euphorbiaceae	<i>Celaenodendron mexicanum</i> Standl.	n.a.	Martijena 1998
	Neotropics	Fabaceae	<i>Mora gonggrijpii</i> (Kleinh.) Sandwith	117.21*	Connell & Lowman 1989
	Neotropics	Fabaceae	<i>Mora oleifera</i> Ducke	n.a.	Holdridge et al. 1971
	Neotropics	Fabaceae	<i>Pentaclethra macroloba</i> Kuntze	5.19	Connell & Lowman 1989
	Neotropics	Fagaceae	<i>Quercus oleoides</i> Schltld. & Cham.	n.a.	Boucher 1981
	Neotropics	Moraceae	<i>Brosimum rubescens</i> Taub.	n.a.	Marimon et al., 2001
	Oceania	Fagaceae	<i>Nothofagus aequilateralis</i> (Baum.-Bodenh.) Steenis	n.a.	Read et al. 2006
	Oceania	Fagaceae	<i>Nothofagus codonandra</i> (Baill.) Steenis	n.a.	Read et al. 2006
	Low-nutrient	Central Africa	Fabaceae	<i>Microberlinia bisulcata</i> A.Chev.	n.a.
Malesia		Theaceae	<i>Adinandra dumosa</i> S. Vidal	1.10	Sim et al. 1992
Neotropics		Fabaceae	<i>Dicymbe corymbosa</i> Spruce ex Benth.	n.a.	Henkel et al. 2005
Neotropics		Fabaceae	<i>Dimorphandra conjugata</i> Sandwith	n.a.	Richards 1996
Neotropics		Fabaceae	<i>Dimorphandra hohenkerkii</i> Sprague & Sandwith	n.a.	Richards 1996
Neotropics		Fabaceae	<i>Eperua falcata</i> Aubl.	5.74	Forget 1989
Neotropics		Fabaceae	<i>Eperua leucantha</i> Benth.	n.a.	Richard 1996
Neotropics		Fabaceae	<i>Eperua obtusata</i> Cowan	3.40	Coomes & Grubb 1996
Neotropics		Fabaceae	<i>Peltogyne gracilipes</i> Ducke	n.a.	Villela & Proctor 2002

Type	Distribution	Family	Name	Seed weight (g)	Reference
Successional	Neotropics	Sapotaceae	<i>Manilkara bidentata</i> (A.DC.) A.Chev.	1.50**	Richards 1996
	Central Africa	Fabaceae	<i>Guibourtia demeusei</i> (Harms) J.Léonard	n.a.	Hughes & Hughes 1993
	Central Africa	Moraceae	<i>Musanga cecropioides</i> R.Br.	0.80*	Connell & Lowman 1989
	Central Africa	Rhamnaceae	<i>Maesopsis eminii</i> Engl.	1.24**	Eggeling 1947
	Central Africa	Rubiaceae	<i>Mitragyna stipulosa</i> (DC.) Kuntze	n.a.	Hughes & Hughes 1992
	Central Africa, Malesia	Euphorbiaceae	<i>Macaranga</i> spp.	n.a.	Richards 1996
	Central Africa, Neotropics	Bombacaceae	<i>Ochroma</i> spp.	n.a.	Richards 1996
	Malesia	Dipterocarpaceae	<i>Shorea albida</i> Symington ex A.V.Thomas	n.a.	Anderson 1961, 1964
	Malesia	Dipterocarpaceae	<i>Shorea parvifolia</i> Dyer	0.70	Whitmore 1984
	Malesia	Euphorbiaceae	<i>Mallotus</i> spp.	n.a.	Richards 1997
	Neotropics	Cecropiaceae	<i>Cecropia latiloba</i> Miq.	2.00	Parolin et al., 2002
	Neotropics	Cecropiaceae	<i>Cecropia mexicana</i> Hemsl.	n.a.	Richards 1996
	Neotropics	Cecropiaceae	<i>Cecropia sciadophylla</i> Mart.	1.80*	Mesquita et al. 1998
	Neotropics	Euphorbiaceae	<i>Alchornea castaneifolia</i> (Humb. & Bonpl. Ex Willd.) A.Juss.	n.a.	Daly & Mitchell 2000
	Neotropics	Fabaceae	<i>Macrolobium acaciifolium</i> Benth.	1.43	Schöngart et al., 2005
	Neotropics	Fabaceae	<i>Senna reticulata</i> (Willd.) H.S.Irwin & Barneby	13.00	Parolin et al., 2002
	Neotropics	Salicaceae	<i>Salix humboldtiana</i> Willd.	2.00	Parolin et al., 2002
	Neotropics	Sapindaceae	<i>Allophylus edulis</i> Niederl.	n.a.	Richards 1996
	Oceania	Casuarinaceae	<i>Casuarina aff. cunninghamiana</i>	n.a.	Whitmore 1984
	Oceania	Casuarinaceae	<i>Casuarina papuana</i> S. Moore	n.a.	Connell & Lowman 1989
	Oceania	Datiscaeeae	<i>Octomeles sumatranus</i> Miquel	n.a.	Richards 1996
	Oceania	Dipterocarpaceae	<i>Anisoptera thurifera</i> Blume	n.a.	Whitmore 1984
	Oceania	Dipterocarpaceae	<i>Anisoptera polyandra</i> Blume	n.a.	Connell & Lowman 1989
	Oceania	Myrtaceae	<i>Eucalyptus deglupta</i> Blume	0.001**	Richards 1996
	Oceania	Myrtaceae	<i>Metrosideros polymorpha</i> J.R.Forst. Ex Hook.f.	n.a.	Mueller-Dombois 2000
	Pantropical	Ulmaceae	<i>Trema</i> spp.	n.a.	Richards 1996
	Tropical Australia	Myrtaceae	<i>Backhousia bancroftii</i> F.M.Bailey	n.a.	Connell & Lowman 1989
Water-logged	Central Africa	Rubiaceae	<i>Mitragyna stipulosa</i> (DC.) Kuntze	n.a.	Richards 1996
	Neotropics	Arecaceae	<i>Mauritia flexuosa</i> L.f.	19.00	Holm et al., 2008
	Neotropics	Fabaceae	<i>Mora excelsa</i> Benth.	61.65	Beard 1946
	Neotropics	Fabaceae	<i>Prioria copaifera</i> Griseb.	28.02	Holdridge et al. 1971
	Neotropics	Fabaceae	<i>Pterocarpus officinalis</i> Jacq.	1.80	Janzen 1978

Following Connell & Lowman (1989) and Hart *et al.* (1989), a growing number of observational studies have examined the various ecological hypotheses presented to obtain a general understanding of monodominant forests (e.g., Torti *et al.* 2001). Numerous life-history traits that enhance monodominance have been hypothesized but there is still a lack of consistency among possible mechanisms and the empirical evidence for each. Here, I evaluate theoretical mechanisms in the light of available evidence from experimental and observational studies and propose a new probabilistic framework to help understand these systems.

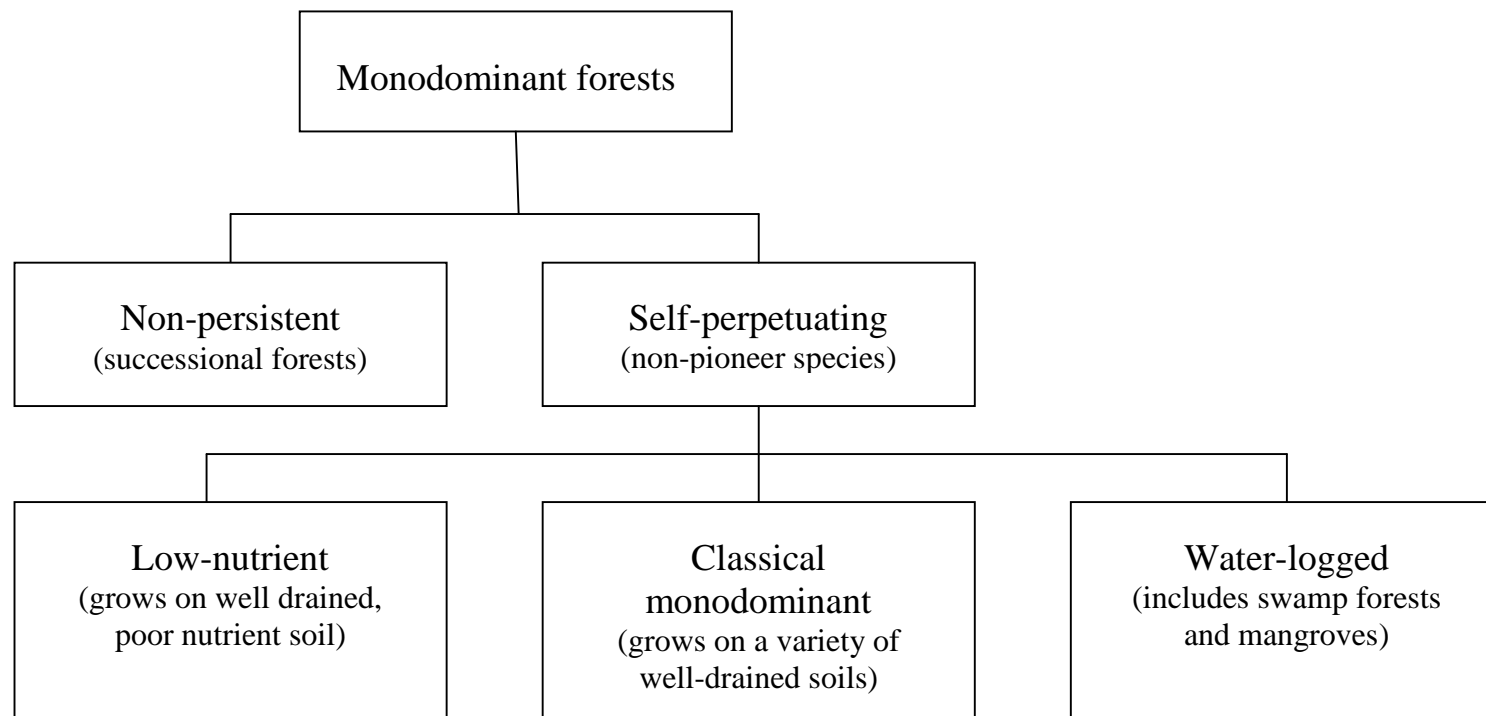
1.3.1. Diversity of monodominance in tropical lowland forests

Monodominant forests can be divided into those that are non-persistent and those that are persistent (Fig. 1.1). Persistent forests that are dominated by a single species can be further divided into three types: water-logged forests, low-nutrient forests and classical monodominant forests. Though this chapter concentrates on the latter type of monodominant forests which I define as those that are found growing under conditions where high-diversity forests are usually found, I summarize the diversity of monodominance in tropical lowland forests as follows:

Successional forests

Non-persistent dominance, by definition, does not have the ability to self-perpetuate under the main dominant canopy, and thus lasts for only one or at most a few generations (Connell & Lowman 1989). However, some monodominant pioneer species, for example *Metrosideros polymorpha* (Mueller-Dombois 2000), can last more than one generation before reaching a regressive phase of decline: I consider these as non-persistent.

Figure 1.1 Types of monodominance in tropical lowland forests.



Short-termed dominance is usually related to secondary forest succession (Hart *et al.* 1989) that occurs following anthropogenic clearance or large-scale natural disturbance such as windstorms (Nelson *et al.* 1994). Although the extant non-persistent monodominant forest cover is not available in literature, the secondary forest succession in the tropics is increasing at a rate of 1.06×10^6 ha per year (Wright 2005). Dominant species in secondary forests can make up 68–89 % of the total number of canopy trees (Connell & Lowman 1989).

Some spatially and ecologically important non-persistent monodominant forests are found in the Neotropics. Seasonal floodplain forests constitute about 3–4 % of the Amazon basin, and about 30 % of these floodplain forests are monodominant (Butler 2006). Examples from these ecosystems are pioneer *Ceropia* spp., *Salix humboldtiana* and *Senna reticulata* that build monodominant forests on newly created sites by sedimentation process of the river dynamics (primary succession) (Parolin *et al.* 2002). Floodplain forests are also found in Africa at the “cuvette centrale” where the portion of the Congo Basin is low and flat. At the “cuvette”, the monodominant species on muddy soils with slow flowing water is *Mitragyna stipulosa* and the species that dominated forests on the drier sandy soils is *Guibourtia demeusei* (Hughes & Hughes 1992).

A species with a suite of life history traits that allow it to successfully colonize an area after perturbation is likely to result a non-persistent dominant stand as these traits are unlikely to allow regeneration under its own shade (Connell & Lowman 1989). The most conspicuous traits found in these tree species are those that enable massive establishment: tolerance to full sunlight, desiccation resistance, fast growth rate, favourable seed dispersal mechanism, certain mycorrhizal associations and an ability to modify soil chemistry (Connell & Lowman 1989). Other abiotic factors have also been observed to enhance the establishment of single-dominance. For example, edaphic conditions can strongly influence species composition of successional communities (Sim *et al.* 1992).

Some successional forests (non-persistent) have species that are monodominant for more than one generation where successional dynamics are slowed due to low-nutrient status. This holds true especially in the nutrient-poor “igapó” forests in Amazon basin where large

areas are regularly inundated for long periods by floods. However, the mechanisms that lead to monodominance are more complex for some successional species. It is critical to decipher the role of their life-history traits to achieving monodominance if we are to understand them. For example, the associations of long lifespan and slow growth of *Macaranga acaciifolia* are of ecological importance to maintain monodominant stands at unfavourable sites (Schöngart *et al.* 2005). The longevity of such tree species indicates long intervals between regeneration opportunities for this species, which are presumably only possible in exceptional years perhaps following with catastrophic events (e.g., droughts; Wittmann & Junk 2003). Thus, the combination of longevity at unfavourable sites and the regeneration opportunities after catastrophic events linked to climate anomalies may be an important mechanism for successional monodominance in floodplains, where few tree species have the ability to reach very high tree ages (Loehle 1988) and where catastrophic events are often linked to the El Niño phenomenon causing severe floods or droughts (Schöngart *et al.* 2005).

Water-logged forests

Among the persistent monodominant old-growth forests, the more well-known type is the water-logged forests such as mangroves and some swamp forests (Fig. 1.1). A monodominant swamp species, such as *Mora excelsa*, can comprise 63–84% of the total number of canopy trees (Connell & Lowman 1989). The permanently water-logged conditions of these forests might suppress diversity by conferring advantages to a particular high-water tolerant species. The palm *Mauritia flexuosa* is another example for monodominance in flooded woody savannahs and forests in wide regions of the Neotropics (Holm *et al.* 2008).

The occurrence of pure stands of dominant species in zones parallel to the shoreline is a common feature of mangroves. The species dominating a particular zone is determined by the degrees of tidal flooding, salinity gradients and soil texture (Richards 1996). The ability to build anatomical adaptations such as adventitious roots and aerenchyma enables certain mangrove species to overcome problems associated with high sedimentation rates and therefore to occur in

monospecific stands (Richards 1996). Although the global estimate for monodominant swamp forest cover is unknown, mangrove cover *per se* is approximately 8×10^6 ha (Liow 2000).

Low-nutrient forests

Another type of persistent monodominant stand is represented by forests, which grow on podzolized sandy soil or other coarse-grained soils with low nutrient status, known as Amazonian caatinga in Venezuela and heath forests in Southeast Asia (hereafter called low-nutrient forests; Fig. 1.1). To our knowledge, there is no estimate of global low-nutrient forest cover in literature. However, soils of very low chemical fertility (spodosols and psamments) cover 109×10^6 ha where tropical forest occurs (Vitousek & Sanford 1986). A monodominant species in low-nutrient forest, for example *Eperua falcata*, can make up at least 67% of the total number of canopy trees in Moraballi, Guyana (Connell & Lowman 1989). The Amazonian caatinga in Venezuela was, however, dominated by *Eperua obtusata* (Coomes & Grubb 1996).

Although low-nutrient forests can be found adjoining mixed forests, the former are strikingly different in plant species richness and composition from the latter (Richards 1996). Taking into account that the substrate of low-nutrient forests is coarse-textured with low water-holding capacity, and the frequent occurrences of irregular droughts with varying intensity in the low-nutrient forests, Brünig's (1974) drought hypothesis asserts that the poor water-retaining capacity of the soils is the main factor in determining the monodominance of the low-nutrient forests, and predicts that the various physiognomic features of the dominant species such as relatively small-sized leaves, light colour and shiny leaf surface would tend to decrease water loss during drought periods by directly or indirectly reducing evapotranspiration, and thus diminishing the impact of water stress in dry weather on the vegetation. However, this hypothesis has been strongly contested by others. For example, many low-nutrient forests that occur in Borneo and South America are not subjected to unusually dry conditions (Richards 1996). The attention once given to the drought hypothesis has now largely shifted to the nutrient deficiency hypothesis, as proposed by Medina *et al.* (1990). The nutrient deficiency hypothesis

suggests that the poor nutrient content in the soils is an important factor in determining the occurrence of the monodominance. Compared with the drought hypothesis, nutrient deficiency hypothesis makes a stronger prediction about the importance of ectotrophic mycorrhizas, a prominent feature in the root systems of dominant trees in low-nutrient forest, providing a direct pathway of nutrient absorption from the litter to the roots. This is because soils in low-nutrient forest generally have lower base-exchange capacity and lower amount of available soil nitrogen (N) due to the low rate of decomposition of organic matters (Medina *et al.* 1990). Nevertheless, like the drought hypothesis, the nutrient deficiency hypothesis has little direct experimental evidence to support it and the basis of the argument relies much on the adaptive physiognomy and floristic features of low-nutrient forest vegetation (but see Coomes & Grubb 1998 which provided experimental evidence that some low-nutrient forest species could tolerate poor soil conditions).

Alternatively, it has been suggested that the toxicity of relatively high concentrations of certain soil elements may play an important role for the dominance of a single species in lowland tropical forest (e.g., Marimon *et al.* 2001; Vilella & Proctor 2002). However, such claims are speculative and there is currently no experimental evidence showing that the tolerance of toxic concentrations of soil nutrients accounts for monodominance (Nascimento *et al.* 2007).

Classical monodominant forests

Besides water-logged and low-nutrient forests, there is another type of persistent monodominant forests which grows in the similar environmental conditions as their adjacent high-diversity forests apparently not caused by major edaphic differences or recent disturbance (hereafter called classical monodominant forests) (Fig. 1.1). They are found in a variety of substrates ranging from low to high nutrient status. The best-studied of the classical monodominant forest is dominated by *Gilbertiodendron dewevrei*, which forms sometimes extensive stands on the plateau of central Africa (e.g., Torti *et al.* 2001). Nevertheless, surprisingly little is understood

about their basic biology. Though the extent of classical monodominant forest cover on global level is not known, *G. dewevrei* probably covers a larger area than any other single-dominant species (Richards 1996). Classical monodominant forests often exist alongside mixed forests with sharp boundaries and can achieve up to 100% dominance in terms of total number of canopy trees (Connell & Lowman 1989). The total species richness of the two forest types is generally similar, except for the presence or absence of classical monodominant species (Connell & Lowman 1989). Examples of classical monodominant species in Southeast Asia and Neotropics are *Shorea albida* (Anderson 1961) and *Peltogyne gracilipes* (Villela & Proctor 2002), respectively (see Table 1.1).

1.3.2. Explaining classical monodominance

At least 21 tree species from 8 different families are considered potentially classical monodominant species (Table 1.1). The existence of monodominant stands of these species in environments which appear to be very similar to those of near-by high-diversity forests has yet to be fully explained. One common assumption regarding classical monodominant forests is that they have experienced little or no disturbance over long periods of time (Connell & Lowman 1989; Hart *et al.* 1989). On the other hand, others have argued that a high frequency of small-area disturbance may lead to monodominance because the small gaps would be colonized by the previously suppressed offsprings of surrounding dominant species (*sensu* Connell's intermediate disturbance theory; Newbery *et al.* 2004).

Torti *et al.* (2001) proposed a suit of life history traits necessary for gaining recruitment advantages over other species to attain monodominance. Plant traits proposed include a high canopy density that casts deep shade to out-compete light-demanding species; slow leaf litter decomposition that creates a physical barrier caused by the accumulation of leaf materials and thereby prevents the establishment of small-seeded species; shade-tolerant saplings that enable survival and growth in the shade created by parent trees; ballistic dispersal that promotes gregarious habits for replacing individuals of other species; and large seeds which contain

enough reserves to pass through the deep litter layers and enable survival at low light levels.

Below I evaluate how well each of these mechanisms that may explain classical monodominance matches the existing empirical evidence. Admittedly, quantitative methods such as meta-analysis can potentially yield much more information than the narrative review presented here. However, rigorous evaluations of the benefits provided by the proposed suite of traits are rare as only a small number of papers have tested the proposed mechanisms of classical monodominance in tropical lowland forests. There are too few studies and too many mechanisms to utilize meta-analytic techniques. Research papers on classical monodominance published since 1989 study only a few species, mainly *Gilbertiodendron dewevrei* and *Celaenodendron mexicanum*. In my assessment of each potential explanation of classical monodominance, the discrepancy between a particular mechanism and the existing empirical evidence should not be considered as a refutation of the relevance of a particular mechanism in general. The existence of counterexamples may merely mean that that particular mechanism alone is not sufficient to explain all monodominance in tropical lowland forests on non-extreme environmental sites.

Mechanism 1: Slow decomposition rate

The distribution of forest types may be closely related to soil conditions such as soil nutrient cycling and availability, nutrient accumulation and release, soil types and drainage (Richards 1996). Soil conditions under monodominant forests (i.e., exogenous condition) and monodominant species (i.e., endogenous conditions) may both give rise to slow decomposition (Torti *et al.* 2001). Torti *et al.* (2001) show that the litter decomposition rate in monodominant *Gilbertiodendron* forest is two to three times slower than that in the mixed forest in central Africa (also see Chapter 6), and suggest that slow decomposition rate may lead to monodominance.

Although the lower litter decomposition rate in the single-species dominant stands might result in the nutrients being slowly released in these forests, there is no evidence showing

that soil properties between classical monodominant forests and their adjacent mixed forests are significantly different. For example, soil surveys conducted in the Democratic Republic of the Congo show no differences in *Gilbertiodendron* forests and their adjacent mixed forests in respect to soil pH, carbon, nitrogen, phosphorus, calcium, magnesium and potassium (Conway 1992; Hart 1985; Hart *et al.* 1989; also see Chapter 2). Further, there were also no edaphic differences in *Nothofagus*-dominated and *Peltogyne gracilipes* dominated forests when compared with their mixed counterparts (Nascimento & Proctor 1997b; Read *et al.* 2006).

Mechanism 2: Large seed in deep leaf litter

Concomitant with a slow rate of litter decomposition is a larger litter standing crop in monodominant forests. It has been suggested that the deep leaf litter depth may prevent seed germination and establishment by acting as a physical barrier to the soil, reducing light availability, changing soil temperatures and also releasing chemical inhibitors during its decomposition (Torti *et al.* 2001). Therefore, species possessing large seeds may have advantages over smaller-seeded species and may be less constrained by the deep litter layer (Torti *et al.* 2001). But again, an average large seed size is not sufficient to explain monodominance on its own for two reasons. First, many large-seeded forest species that occur in mixed forest adjacent to monodominant forest do not form monodominant stands themselves. In central Africa, these include *Anonidium mannii*, *Mammea africana* and *Uapaca paluosa*, and in South America, *Aldina latifolia*, *Swartzia polyphylla* and *Vatairea guianensis*. Second, some monodominant species could also have small seeds (e.g., *Dryanobalanops aromatica*; see Table 1.1). Moreover, Martijena (1998), using both greenhouse and field experiments, has shown that germination percentage and seedling survival of a mixed forest species, *Caesalpinia eriostachys* (average dried seed weight: 0.22 g; Liu *et al.* 2008) were not affected by the thick litter of monodominant *Celaenodendron mexicanum* (average dried seed weight: 0.64 g; Liu *et al.* 2008). This suggests that non-dominant species may, at least to some degree, be able to withstand the negative effects of deep litter of monodominant stands.

Mechanism 3: Ectomycorrhizal association

The mycorrhizal hypothesis, described by Connell & Lowman (1989), considers the benefits of possession of EM associations as a key factor characterising monodominant species. They found that many single-dominant tree species were found to be associated with EM (see Connell & Lowman 1989). EM infection may allow more efficient exploitation of larger volumes of soils or directly decompose leaf litter and take up organic nitrogen (Connell & Lowman 1989). In addition, EM may allow their host to mast fruit (see Mechanism 4) by supplying a necessarily large amount of P from storage fungal hyphae (Turner 2001).

However, there is no clear evidence of classical monodominance arising through an association with EM. Martijena (1998) observed that the classical monodominant *Celaenodendron mexicanum* which occurs in Mexico is associated with vesicular-arbuscular mycorrhizae rather than EM. This implies that an EM association is not always necessary for monodominance to occur. Moreover, there are a number of other non-EM associated tree species, such as *Cynometra alexandri* that under some circumstances can attain monodominance (Torti *et al.* 1997). Conversely, EM-associated tree species are present in mixed forests adjoining monodominant forests, for example *Julbernardia seretii* of which there is little evidence of it out-competing other species over large areas (Hart 1995). Lastly, the presence of some monodominant stands is difficult to explain by the purported beneficial mechanism provided by EM because the soils on which they stand are not necessarily poorer in nutrients than nearby areas that are not dominated by a single species (as discussed in Mechanism 1).

Mechanism 4: Masting and ballistic seed dispersal leading to predation satiation

Many monodominant tree species are masting species. Synchronous supra-annual flowering is a characteristic of these species that results in synchronous supra-annual fruiting. Several authors have thus hypothesized that mast fruiting and irregular periodicity to reproduction are important reproductive traits for many tree species to attain monodominance (e.g. Torti *et al.* 2001). This

is because the amount of fruit available at a particular site at a particular time is more than can be eaten by the population of seed predators, thus increasing offspring survivorship (Torti *et al.* 2001). In addition, Turner (2001) suggests that irregular seed production might keep populations of seed predators small. Thus, only a few individuals would be present to eat the many fallen seeds during episodic masting. Indeed, Boucher (1981) has shown that the seed survivorship of the monodominant tropical lowland oak, *Quercus oleoides*, is inversely proportional to the seed predator density within masting areas. In contrast to the predator satiation hypothesis, the escape hypothesis, coined by Howe & Smallwood (1982) is proposed to counter such survival. This hypothesis predicts high seed mortality for mast fruiting because clumps of fruits are much easier to locate by the seed predator, even though some seeds 'escape' being depredated as the predators are non-perfect seed locators. Evidence seems to be in favour of the escape hypothesis. For example, Clark & Clark (1984) observed the seed survivorship near a parent tree was low as all the seeds were being destroyed. Furthermore, evidence from stands of *G. dewevrei* only partially supports predator satiation hypothesis. Hart (1995) have found that in masting areas of *G. dewevrei* forest, where seed densities were high, mammalian predators were satiated, but not the specialized insect predators. Insect seed predators are probably less likely to be satiated by mast fruiting due to their short regeneration times which allow large populations to be built up in short period to exploit the available food resources (Turner 2001). Moreover, compared with mammalian predators who are frequently opportunistic foragers, most insect predators are highly specialized and are able to track the masting areas of potential host and infest a high number of seeds (Hammond & Brown 1998). Hart (1995) thus suggested that mast fruiting does not directly determine higher canopy dominance of *G. dewevrei*. On the other hand, researchers have found no evidence to support escape hypothesis in a monodominant *Mora gonggrijpii* stand based on insect seed predation (Hammond & Brown 1998). More research is therefore required to establish why the effects of seed predators on masting seed survivorship are so variable across studies.

Apart from masting, the gregarious habit of *G. dewevrei* under parental trees due to poor seed dispersal does not seem to be uniquely advantageous as claimed by Torti *et al.*

(2001). Like *G. dewevrei*, *Julbernardia seretii* of the mixed forest also has ballistic dispersal and its seeds germinate within a week of explosive dehiscence of the pods (Hart 1995). However, *J. seretii* was not observed to be a dominant species. In general, this trait may be necessary for attaining monodominance but is not sufficient to explain it.

Mechanism 5: Shade tolerance under closed canopy

A few studies have provided circumstantial evidence for a relationship between seedling survival under the forest canopy and monodominance. For example, Hart (1995) reported that *G. dewevrei* seeds suffer higher mortality in the forest understorey but surviving seedlings exhibited a greater persistence in the understorey, thus achieving a higher density with increasing seedling size and age compared to *Brachystegia laurentii* (Hart *et al.* 1989) and *J. seretii* (Hart 1995) from the mixed forest. Although these studies did not further investigate which mechanisms may confer greater persistence of *G. dewevrei* in the forest understorey, there is a deduction we can make with some confidence: because *G. dewevrei*, *B. laurentii* and *J. seretii* can all withstand low-light environments and are able to germinate and establish in the shade of their respective parent trees (Hart *et al.* 1989; Hart 1995), it seems unlikely that the deep canopy and shade tolerant property of *G. dewevrei* are the unique features underlying the greater seedling recruitment in *G. dewevrei* stands. Moreover, the understorey of a monodominant forest does not always have lower understorey light levels than that of the adjacent mixed forest (Martijena 1998), although this is likely to be the case for *G. dewevrei* stands (Vierling & Wessman 2000).

Mechanism 6: Escape from herbivory

Conceptually related to Mechanism 4, the leaf defence hypothesis considers low leaf damage of dominant saplings leading to an increase in their survivorship to achieve monodominance. The resistant to herbivory and pathogen damage is achieved by the large investment in leaf defence. As first proposed by Janzen (1974), an aggregated distribution of a given species should induce

a strong selective pressure and promote enhanced foliage defence against natural enemies. This is because of an increased probability of specialised herbivores and pathogens presence due to the high concentration of resource in an area. The most conspicuous leaf defences are high phenolic compound and tough fibre content in leaves (Turner 2001).

The only test of leaf defence hypothesis relating to monodominance is an observational study of *G. dewevrei* dominated forest by Gross *et al.* (2000). Gross *et al.* (2000) surveyed the rate of leaf damage of the monodominant *G. dewevrei* and seven other tree species within both monodominant and adjacent mixed forests, and found that *G. dewevrei* suffered a higher level of leaf damage than the other species. Furthermore, contrary to leaf defence hypothesis, *G. dewevrei* did not have a higher level of phenolic content as compared to the other species. Although it had higher fibre content, the fibre content did not correlate with herbivore damage. This study demonstrates that the establishment and maintenance of monodominance was not dependent on the avoidance of herbivory and pathogen damage.

A case of dominant tree species suffering intense herbivory by defoliating insects is reported by Maisels (2004). In this study, Maisels (2004) observed the defoliation of a monodominant stand of *Aucoumea klaineana* by a lepidopteran species in Gabon. While leaf defence hypothesis might possibly prevent the damage from some generalist herbivores, there is very little evident that it is the main mechanism on which species depends upon for attaining or maintaining monodominance.

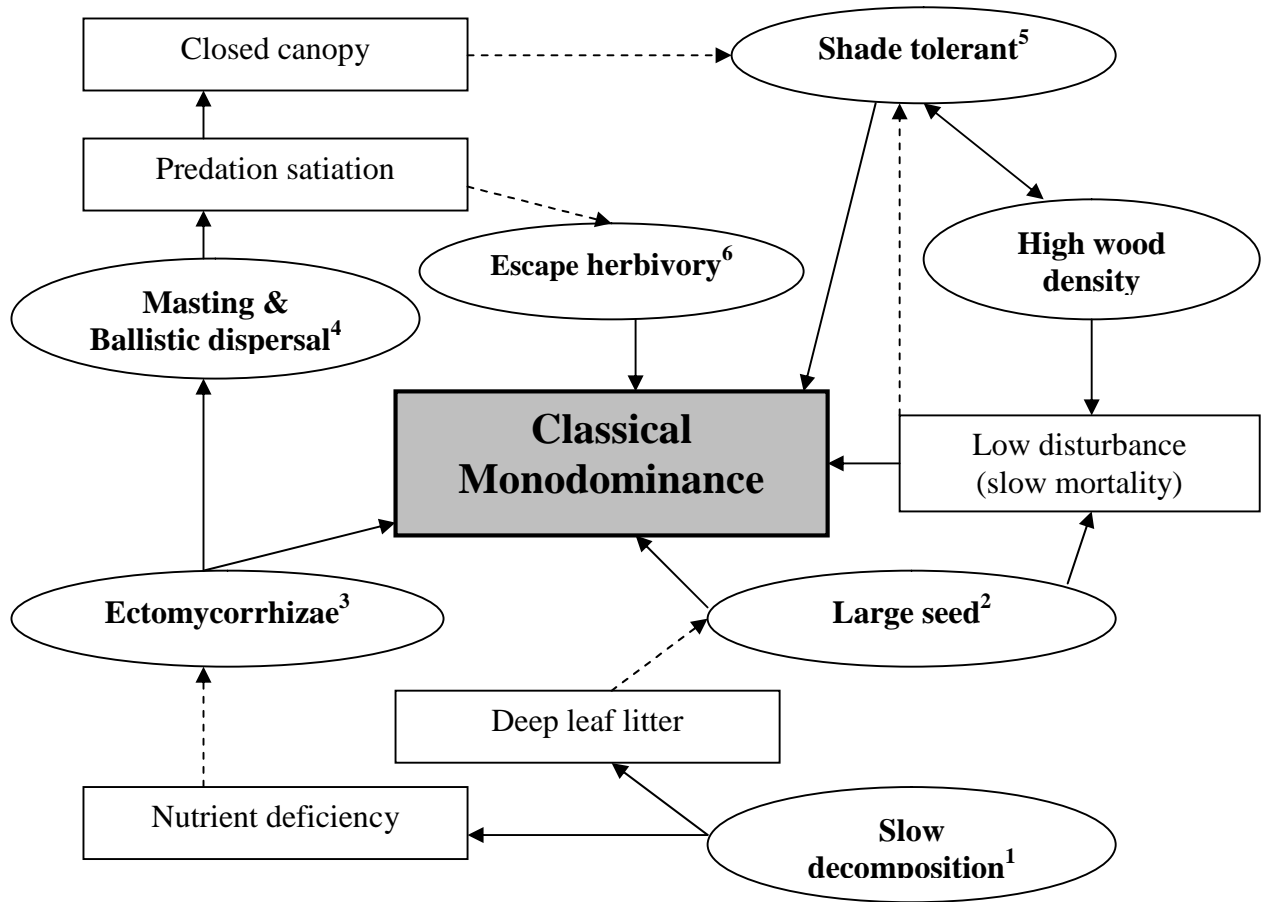
1.3.3. Linking the hypotheses: a new framework

There has been a considerable effort to apply ecological theory to questions relating to the existence of monodominance. Collectively, the body of evidence has led to the perspective that a particular life-history trait could enable a species to increase its growth and survival relative to other species, and therefore out-compete other species under either small-scale or no disturbance regime. Thus, monodominance of a species is the result of the “endogenous” characteristics of the particular species (i.e., the species traits and their implications) *and* the

“exogenous” characteristics of the forest system (i.e., absence of externally-imposed large-scale disturbance). However, the theory and empirical studies are inconsistent (Fig. 1.2). In short, there is no “single” magic bullet trait that enables a tree species to attain monodominance.

Nevertheless, based on these ideas, I suggest a new probabilistic conceptual framework where a suite of potential positive feedbacks may lead to a high probability of monodominance being attained (Fig. 1.2). That is to say, some traits possessed by a potentially dominant species can lead to additional and enhanced conditions that favour the establishment of greater numbers of the same species, leading to a new monodominant system. The possible feedback mechanisms identified include shade-tolerance and being able to produce large seeds. These in turn, are favoured by environmental factors such as deep shade under the forest canopy and a deep leaf litter layer, respectively (ter Steege & Hammond 2001; Torti *et al.* 2001). In addition, ectomycorrhizal associations, which may allow plants with such associations to out-compete those without them in low nutrient environments with slow litter decomposition (Connell & Lowman 1989), and predation satiation, which may result from masting (Boucher 1981), may both further increase the probability of monodominance (Fig. 1.2). Such ectomycorrhiza-mediated nutrient cycling mechanisms may further enhance monodominance by helping to replenish limiting elements lost to masting (Henkel *et al.* 2005) and increasing seedling survivorship near parent trees (McGuire 2007), further facilitating persistent monodominance. Furthermore, species with traits such as shade tolerance, high wood density and large seeds on average also have low mortality rates intrinsically (Chao *et al.* 2008; Foster & Janson 1985), therefore creating low-disturbance conditions that are conducive for the establishment of monodominance.

Figure 1.2 Model of possible mechanisms (ovals) and their consequences (boxes) leading to persistent monodominance in tree species that grows in environmental conditions similar to adjacent high-diversity forests. Arrows with dashed line point to mechanisms that are beneficial in the environmental conditions created by other mechanisms.



Hypothesis/ Mechanism	References	
	Support	No evidence
1	Torti <i>et al.</i> 2001; Whitmore 1984	Torti & Coley 1999; Read <i>et al.</i> 2006
2	Hart <i>et al.</i> 1989; Torti <i>et al.</i> 2001	Hart 1995; Martijena 1998
3	Connell & Lowman 1989; Martijena 1998	Torti <i>et al.</i> 1997
4	Boucher 1981; Nascimento & Proctor 1997	Hart 1995
5	Torti <i>et al.</i> 2001	Hart <i>et al.</i> 1989; Mueller-Dombois 2000
6	Torti <i>et al.</i> 2001	Gross <i>et al.</i> 2000; Maisels 2004

This probabilistic framework, based on empirical support, links all six potential mechanisms into a potentially self-reinforcing cycle, potentially allowing apparently contradictory observational and experimental results to be reconciled. However, the external factors such as low occurrence of natural disturbance also determine the likely probability of establishment of monodominant forest stands. For example, Hart *et al.* (1989) suggest that monodominant forests might indicate areas that have not experienced large-scale disturbance for long periods as such disturbance would open the canopy; therefore shade intolerant species may out-compete species that usually attain classical monodominance. Hence, the lack of disturbance, together with the favourable microhabitat created by the species itself, are likely to be needed for a single species to out-compete all others over substantial areas.

1.4. Thesis synopsis

My thesis is a landscape scale study in tropical forest of the Dja Faunal Reserve, Cameroon, focusing on two linked parts: (1) to enhance our understanding of monodominant *Gilbertiodendron dewevrei* forest, and (2) to test the diversity-function relationship in tropical forests utilizing a natural experiment of involving forests with differing diversity. The physical (soil pH, bulk density, particle size) and chemical properties (23 elements including carbon, nitrogen, phosphorous, aluminium, calcium, magnesium, sodium) of the soils from monodominant forest and its adjacent mixed species forest were quantified in order to test whether the edaphic conditions were plausible factors for controlling tree diversity in the monodominant forest. I investigated the influences of tree life history traits (tree height at maturity, maximum diameter at breast height, primary seed dispersal mechanism, relative abundance, light requirement, wood density, and geographical distribution) in controlling tree diversity in the monodominant forest of *Gilbertiodendron dewevrei*. Phylogeny was controlled for by including family as a covariate in statistical modelling.

I collated a forest data set of field measurements of above-ground biomass (AGB) growth, litterfall productivity, net primary productivity (ANPP), decomposition rate, with

accompanying tree species diversity data (species richness, Simpson's diversity index, species evenness) from two forest types of contrasting diversity (low-diversity monodominant forest and high-diversity mixed-species forest) to undertake a landscape scale analysis. Trap species number index (an indicator of species richness in the vicinity of the litterfall traps) was additionally available for a subset of quadrats in the study plots. I investigated the nature and strength of the ecosystem functions (AGB growth, litterfall productivity, ANPP, stability in litterfall production and decomposition rate) along a natural gradient of tree species diversity within each forest type in order to identify if species diversity is a significant controlling ecological factor for ecosystem functioning. I also compared the diversity-functioning relationships between the two forest types in order to determine if the effects of species diversity on functioning are similar between two adjacent forest types.

1.5. Thesis aims and objectives

Thesis aim: to quantify the relationship between tree species diversity and ecosystem function in a low-diversity forest (monodominant forest) and its adjacent high-diversity forest (mixed forest).

*Objective 1: To determine the soil properties in monodominant *G. dewevrei* forest and its adjacent mixed forest (Chapter 2).*

1.1. To compare soil properties between the monodominant forest and its adjacent mixed forest.

*Objective 2: To determine the species diversity of tree (diameter at breast height ≥ 10 cm) in monodominant *G. dewevrei* forest (Chapter 3).*

2.1. To compare species richness parameters between the monodominant and mixed forests.

2.2. To identify the key life-history traits driving the establishment of non-dominant species in the monodominant forest.

Objective 3: To determine the effects of tree species diversity on forest AGB and productivity (Chapter 4).

- 3.1. To estimate AGB of the monodominant and mixed forests.
- 3.2. To estimate litter productivity and ANPP of the two forest types.
- 3.3. To quantify the relationship between tree species diversity and productivity (AGB growth, litterfall productivity and ANPP) for each forest type.

Objective 4: To determine the effects of tree species diversity on temporal variability of litterfall mass (Chapter 5).

- 4.1. To compare the biomass allocation between the two forest types.
- 4.2. To compare the litterfall phenology between the two forest types.
- 4.3. To quantify the relationship between climatic factors and litterfall phenology.
- 4.4. To quantify the relationship between tree species diversity and temporal variability of litterfall mass for each forest type.

Objective 5: To determine the effects of tree species diversity on leaf litter decomposition rate (Chapter 6).

- 5.1. To estimate the decomposition rates in the monodominant and mixed forests by direct observations.
- 5.2. To estimate the decomposition rates in the two forest types by *in situ* litterbag experiments.
- 5.3. To quantify the relationship between tree diversity and litter decomposition.
- 5.4. To compare the role of litter mixture on decomposition rate between the two forest types.

2. Soil properties of low-diversity monodominant forests and adjacent high-diversity mixed forests in south-eastern Cameroon

2.1. Introduction

There are large areas of tropical lowland forests being dominated by a single tree species despite tropical forests often being perceived as systems with highly diverse and complex communities. Soil properties are known to influence forest species distributions (e.g., Clark *et al.* 1995). The importance of edaphic conditions in the spatial distributions of tropical tree species has been well studied (e.g., Veenendaal *et al.* 1996). In contrast, there are few studies looking at the role of soil properties in the spatial distribution of the low-diversity tropical forests, often termed ‘monodominant forests’, and the potential influence of the availability of nutrients for plant uptake in determining their occurrence, in comparison to the adjacent high-diversity mixed forests (e.g., Nascimento & Proctor 1997a; Newbery *et al.* 1997).

In central Africa, the low-diversity forests are often dominated by *Gilbertiodendron dewevrei*, a highly shade tolerant species that occurs in the central Congo basin and its surrounding plateau. While some monodominant stands grow only on nutrient-poor soils, the monodominant *G. dewevrei* is able to grow on a variety of soil conditions ranging from water-logged to well-drained substrates and, in addition, has been found to grow on a wide spectrum of soil fertility from the nutrient-poor white sand soils to richer clayey soils (e.g., Conway 1992; Hart *et al.* 1989; for details of monodominant *Gilbertiodendron* forest, see Chapter 1).

It has been suggested that soil-related mechanism may play a role in the formation of monodominant forests (e.g., Torti *et al.* 2001). In a study investigating the phenomenon of monodominance, Torti *et al.* (2001) proposed that in the *Gilbertiodendron*-dominated forests, having low nutrient turnover is one of the prerequisites to achieve monodominance. One way to achieve the slowing of nutrient turnover is to produce poor-quality leaf litter that is slow to decompose. The resulting slow rate of nutrient turnover may then lower the nutrient availability to plants and in turn affect the survival of some other species in the *Gilbertiodendron* forests.

Torti *et al.* (2001) found that the leaf litters in the *Gilbertiodendron* forests tended to accumulate to a mass of three times more than that of nearby mixed forests (also see Chapter 6). Concomitant with litter accumulation is a lower rate of decomposition in the *Gilbertiodendron* forests in which leaf litter decomposed two to three times slower in the monodominant forests than in the mixed forests (Torti *et al.* 2001; also see Chapter 6).

Nevertheless, in studies of soil properties of other monodominant forests, Read *et al.* (2006) found no evidence that the soil determines the boundaries between *Nothofagus*-dominated forest and adjacent mixed forest in New Caledonia. Similarly, Martijena (1998) found that there were no significant differences in soil properties between monodominant forest of *Celaenodendron mexicanum* and adjacent high-diversity forest in Mexico. However, the results from studies of *G. dewevrei* have proven inconclusive. For example, Conway (1992) has showed that there were no significant differences in the studied soil parameters between *Gilbertiodendron* forest and adjacent mixed forest in the Democratic Republic of the Congo, whereas in the same study area, Torti *et al.* (2001) have reported that the nutrient supply rate of ammonium and nitrate in the soils of *Gilbertiodendron* forest was lower than those of the mixed forest. Thus, I suggest that the lack of association between soil properties and the occurrence of the *Gilbertiodendron* forests remains equivocal.

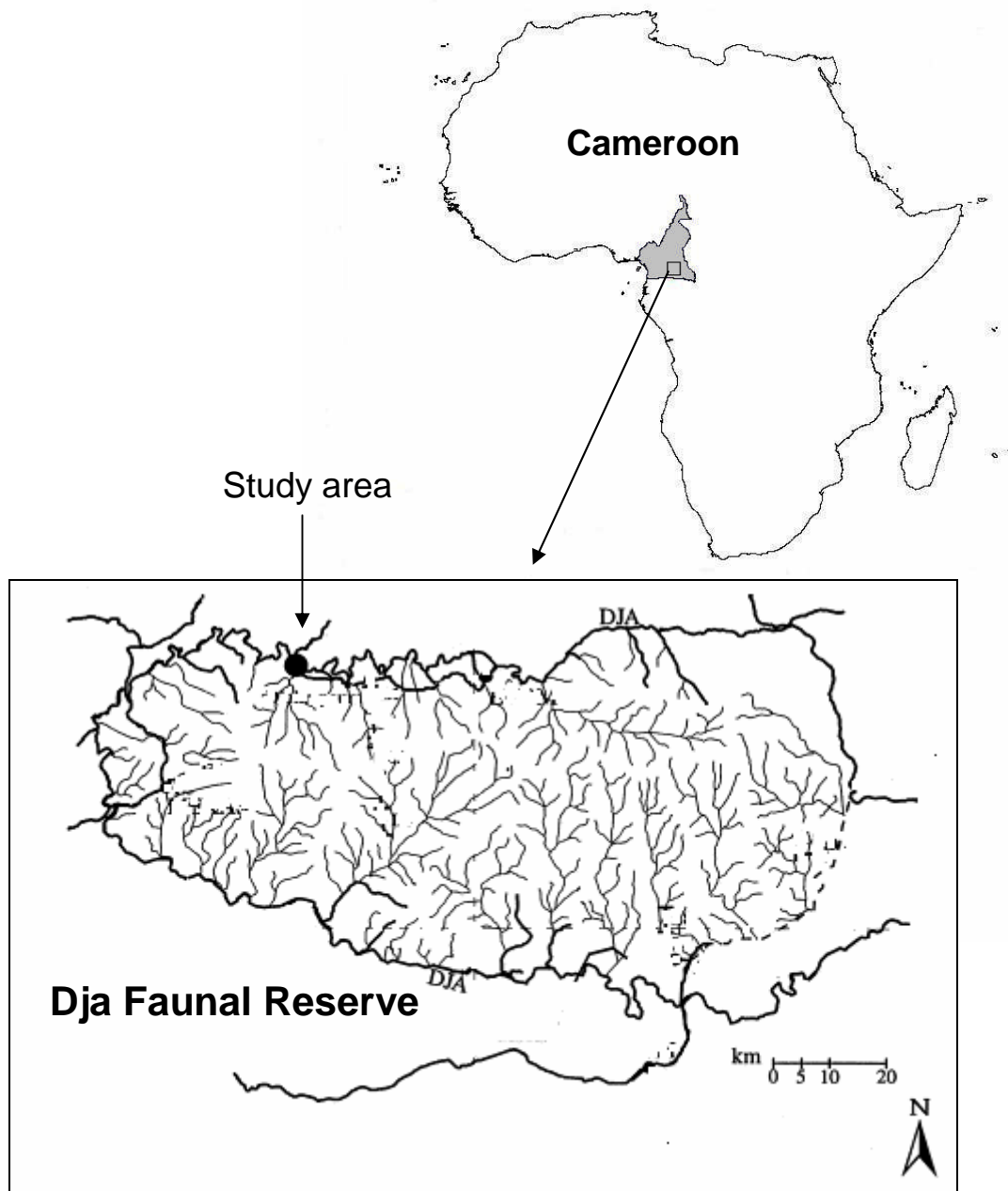
Given the large amount of litterfall accumulated on the ground of the *Gilbertiodendron* forests, and their slow decomposition rates of the leaf litters, it follows that these litters may release nutrients more slowly into the soils and perhaps change the top soil properties (upper few centimetres) of these forests. In this study, I investigated the physical and chemical soil properties from the *Gilbertiodendron* forests (hereafter called the monodominant forests) and the adjacent high-diversity forests (hereafter called the mixed forests) to test whether there are differences in soil properties between the two forest types both near surface and far from the surface. Potential differences in soil properties between the two forest types may explain the distributions of *G. dewevrei* within the central African forest. Further, differences in soil properties may explain some differences in ecosystem functioning such as net primary productivity differences between the two forest types.

2.2. Methods

2.2.1. Study area

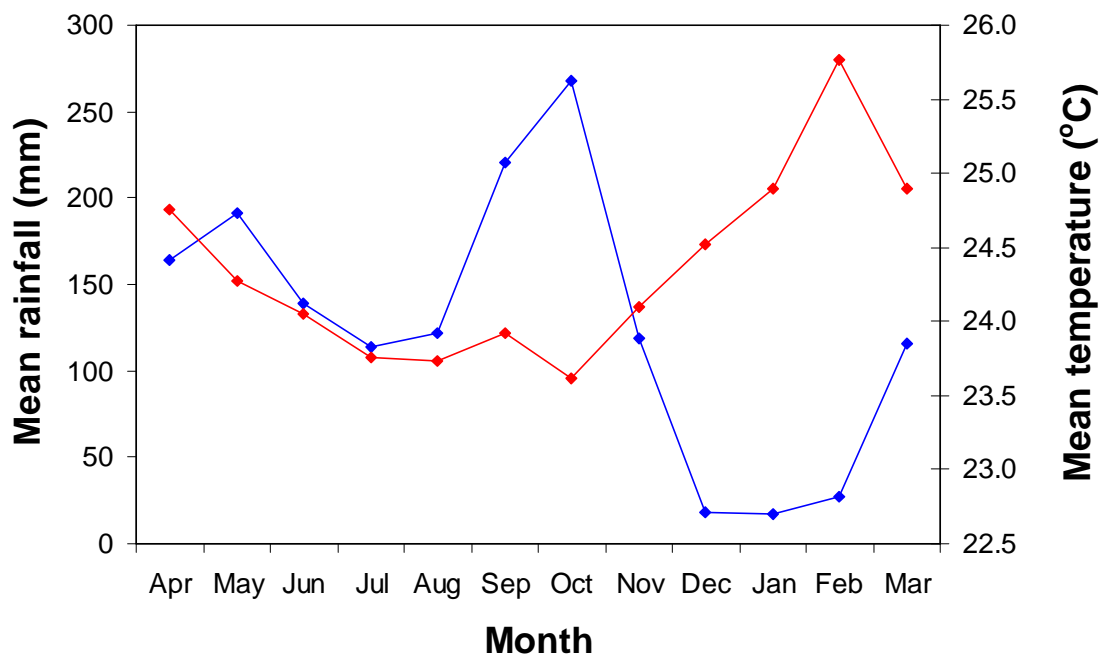
My study was conducted at the Dja Faunal Reserve (hereafter called the reserve), located between 2°49'–3°23'N and 12°25'–13°35'E in south-eastern Cameroon (Fig. 2.1; McGinley 2008). The reserve was established in 1950 and is one of the largest protected rain forest areas in Africa (McGinley 2008). The reserve covers an area of 526000 ha, which consists of lowland moist evergreen tropical forests at an elevation between 400–800 m (McGinley 2008). About two-third of the reserve's perimeter is demarcated by the Dja River, forming a natural boundary. Only the south-east part of the reserve is not being encircled by the Dja River. Such inaccessibility due to the natural barrier offers the reserve protection from large-scale human disturbance. The Dja River flows in an anti-clockwise direction around the reserve and eventually empties into the Sangha River in the Republic of Congo (Wilmé 2002). Within the reserve, there is a complex hydrological network (Fig. 2.1). The nearby towns are Lomie (situated at 5 km to the east of the reserve), Bengbis (about 10 km to the northwest) and Messamena (about 45 km to the north) (Wilmé 2002).

Figure 2.1 Map of study location at the Dja Faunal Reserve in Cameroon.



The climate of the reserve is of equatorial. Based on the meteorological data collected from three locations near the reserve (Akonolinga [2°56'N, 11°57'E], Sangmélina [3°47'N, 12°15'E] and Lomié [3°09'N, 13°37'E]) between 1979 and 2008, the multiannual mean annual rainfall is 1441 mm, 1575 mm and 1520 mm (average value = 1512 mm), respectively. Based on this long-term climate data, the lowest annual rainfall recorded was 745 mm at Akonolinga in 1982 and the highest annual rainfall was 3275 mm at Akonolinga in 1979. The 30-year average monthly temperature and precipitation were not statistically different among the three locations (Friedman test; $P > 0.05$) and therefore I used the average values of the three locations for climate description as being typical for the reserve. The average monthly rainfall ranges from 18 mm in December and January to 268 mm in October (Fig. 2.2). The climate is characterized by two wet seasons with rainfall peaks in May (191 mm) and October (268 mm; Fig. 2.2). The two dry periods are July–August (113–122 mm) and December–February (18–27 mm; Fig. 2.2). The maximum average monthly temperature in the reserve is 25.8 °C in February, and minimum average monthly temperature is 23.6 °C in October.

Figure 2.2 Monthly rainfall (blue line) and temperature (red line) patterns in the Dja Faunal Reserve based on the average of 30 years data from 1979 to 2008.



Crystalline metamorphic rocks, comprising schists, gneisses and quartzite, from Precambrian origin form the underlying substratum of the reserve (McGinley 2008). Soils of the region are often described as clayey and poor in nutrients (e.g., McGinley 2008). Although a recent study by van Gernerden (2003) suggests that lowland rain forests in southern Cameroon may have experienced historical anthropogenic disturbances, the reserve has no evidence of major recent human-induced disturbance (e.g., logging, clearance). The vegetation in the reserve has a main canopy of 30–40 m with tree emergents rising to 60 m (McGinley 2008; also see Chapter 4). Sonké (2004) recorded at least 372 tree species with diameter at breast height (dbh) ≥ 10 cm. The predominance of Euphorbiaceae (18 % of all recorded species) in the reserve is a characteristic commonly shared by African tropical forests elsewhere (Sonké 2004). There are about 58 species that form the basic flora composition of the canopy in the reserve (Sonké 2004). Large naturally-occurring monodominant patches of *Gilbertiodendron dewevrei* occur within the mixed forest throughout the reserve. Although the size of these monodominant forest fragments in the reserve is not known, *G. dewevrei* often extensively dominates on the plateau of central Africa (Torti *et al.* 2001). The common tree species in the mixed forests include: *Anonidium mannii*, *Carapa procera*, *Petersianthus macrocarpus*, *Polyalthia suaveolens* and *Tabernaemontana crassa* (Sonké 2004; also see Chapter 3). Besides the monodominant *G. dewevrei* forest and the mixed forest, there is also swamp vegetation characterized mainly by genus *Eremospatha*, *Laccosperma*, *Oncocalamus* and *Raphia* (Sonké 2004).

The reserve harbours important populations of mammals, including elephants and lowland gorillas (Dupain *et al.* 2004), and birds (Whitney *et al.* 1998). At least 78 species of mammals and 320 species of birds are recorded in the reserve (Wilmé 2002). Communities of nomadic hunter-gatherer Baka indigenous people inhabit the reserve, alongside a small number of sedentary Badjoué, Bantou, Boulou, Fang and Nzimé people who engage in subsistence agriculture near the edges of the reserve (Wilmé 2002).

2.2.2. Plot establishment

The fieldwork for this study was carried out in three independent monodominant forest patches and their adjacent mixed forests using 100 m × 100 m (1 ha) plot surveys. To standardize data collection for comparison with other studies, square plots were chosen over other shapes. Furthermore, square plots have fewer problems with decisions concerning the presence of trees inside or outside the plot edge due to their lower edge/area ratio. All three plots in monodominant forest were located in independent *G. dewevrei* patches identified using satellite images by B. Sonké and S. Lewis. The locations of the *G. dewevrei* patches were at least 4 km apart from each other. For each monodominant forest plot, a corresponding plot was also established in the adjacent mixed-species forest for comparative purposes. The three mixed forest plots were 452 m, 505 m and 818 m away from their *G. dewevrei*-dominated counterparts. In total, six 1 ha plots were set up. See Chapter 3 for the tree species diversity of the two forest types.

2.2.3. Soil sampling

Within each plot, I sampled soils at five stratified-random locations, based on the plot topography, at eight depths: at 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–100 cm and 150–200 cm using a soil auger (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands). At each depth, about 200 g of soils was collected. At a random point along the perimeter of each plot, a soil pit of 2 m deep (about 2 m long and 1.5 m wide) was dug to collect the soil samples at the eight depths. However, due to budget constraint, I selected three of the six sampled locations (five stratified-random locations and one pit), with an aim to represent topographical gradients, from each plot and used five depths (0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm and 150–200 cm). In total, I used soils of five depths at three locations within each of the six plots for the soil analyses.

Before analysis, the samples were air-dried at room temperature and then sieved through a 2 mm mesh. Soil pH was measured using a mixture of 10 g of soil with 25 ml of

deionized water. Readings of the pH meter were taken only after the mixtures were stirred for one hour.

Particle size was measured on the sodium dithionite and sodium citrate treated soil. Mixture of 4 g of soil with 2 g of sodium dithionite, 22 g of sodium citrate and 100 ml of deionized water were shaken overnight and then allowed to settle for 12 hrs. I decanted the liquid and added 100 ml deionized water with 1 g of calgon. The mixture was again shaken for one hour before being introduced to the particle size analyzer (Coulter LS 230, Coulter Electronics Limited). I determined the proportions of clay, silt and sand, and the median value of particle size for each soil sample. I followed the International Society of Soil Science size classes for the soil particle size classification (Brady & Weil 1999): particle size <0.002 mm was classified as clay; ≥ 0.002 mm and <0.02 mm was classified as silt; and >0.02 mm was classified as sand.

Total nitrogen (N) and carbon (C) contents in soils were measured on the finely ground samples using an elemental analyzer (Euro EA, EuroVector instruments and software). I determined the concentrations of aluminium (Al), calcium (Ca), potassium (K), magnesium (Mg) and sodium (Na) in the soil samples by using a single extraction with silver-thiourea for measuring exchangeable cations. The exchangeable cations were extracted for 4 hrs from 5 g samples by 30 ml of silver-thiourea reagent and analysed by inductively coupled plasma optical emission spectrophotometer (Optima S300 DV, Perkin Elmer) (Pleysier & Juo 1980). Concentrations of another 15 elements—boron(B), barium (Ba), cobalt(Co), chromium(Cr), copper(Cu), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni), selenium (Se), silicon (Si), strontium (Sr), titanium (Ti), vanadium (V) and zinc (Zn)—were also measured using the same cation exchange capacity (CEC) procedure. Although this method was not optimal for quantitative analyses of these elements, using a standardized method enabled me to compare the relative quantities of these elements in the soils of the two forest types (Quesada 2009).

Inorganic phosphorus (P) and total P were extracted by a fractionation method in which the former was precipitated with 0.9 M H_2SO_4 and the latter was treated with ammonium persulphate and H_2SO_4 digests on a hotplate (<400 °C) (Quesada 2009). Then the concentrations

of inorganic P and total P were determined by the method following Murphy and Riley (1962). This method uses a mixture of ammonium molybdate, ascorbic acid and antimony potassium tartrate solutions to allow colour development when mixed with the samples. The absorbance of the standards of known P concentrations and coloured samples are then measured on the spectrophotometer set to 712 nm. I also extracted the labile P using resin strips in the mixture of 0.5 g samples with 30 ml deionized water. The resin strips were then removed and soaked in 20 ml 0.5 N HCL before the determination of labile P concentration following Murphy & Riley (1962).

Samples for bulk density determination were collected from the pits at the five depths using container-rings of known volume (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands), and oven-dried at 105 °C. Bulk density was then determined as a measure of the dry weight per unit volume (g/cm^3).

For each of the five soil depths sampled from each plot, the quantitative values of soil properties are reported as the means of the three samples obtained from the respective plot. To examine if there were differences in soil properties between the *Gilbertiodendron* forests and mixed forests, I calculated their mean values and 95% confidence intervals ($n = 3$) for each soil depth, and for the mean value of the top soil depth classes combined (0–5 cm, 5–10 cm, 10–20 cm and 20–30 cm). Then I performed Wilcoxon signed ranks tests to determine further if the soil properties were different between the two forest types.

2.3. Results and Discussion

Based on the Food and Agriculture Organization of the United Nations (FAO) soil classification (<http://www.fao.org/ag/AGL/agll/key2soil.stm>), the soils at all depths from the monodominant and mixed forests were both acidic, weathered clayey ferralsols (equivalent to oxisols in United States' Department of Agriculture soil taxonomy). Soil texture was not different between the monodominant forests and mixed forests (Fig. 2.3, A-C; Table 2.1). The top soils between 0 cm and 30 cm from both forest types were silty clay loam and became silty clay at the depth below 150 cm (Brady & Weil 1999; Fig.2.3, A-C).

Although median soil particle size decreased with depth in both forest types (Fig. 2.4A), the median grain size of all soil samples from the different depths was still classified as silt. Soil pH increased with depth in both forest types (Fig. 2.4B). However, all soil samples were acidic and there was no significant difference between the two forest types (Fig. 2.4B; Table 2.1). Similarly, higher soil bulk density was observed in greater depth in both monodominant forests and mixed forests, and there was no difference between the forest types (Fig. 2.4C; Table 2.1). Decreasing with soil depth, the C content (Fig. 2.5A), N content (Fig. 2.5B), labile P concentration (Fig. 2.6A), inorganic P concentration (Fig. 2.6B) and total P concentration (Fig. 2.6C) were not different between the two forest types (Table 2.1). The C/N ratios of all soil samples from different depth ranged below 25:1 and were not different between both forest types (Fig. 2.5C; Table 2.1). Likewise, the bulk densities of the top and deep soils were not different between the two forest types.

Concentrations of Al, Ba, Ca, Cu, Fe, K, Mg, Mn, Na, Ni and Zn along the depth gradient were not different between the monodominant forests and the mixed forests (Fig. 2.7 & 2.8; Table 2.1). Concentrations of Ba, Mg and Ni in the monodominant forests were constantly, but non-significantly, lower than in the mixed forests (Fig. 2.7 & 2.8; Table 2.1). Concentrations of other eight elements—B, Co, Cr, Mo, Se, Sr, Ti, and V—were at too low level to be detected by the CEC method.

Table 2.1 Soil physical and chemical characteristics in three 1 ha plots of monodominant *Gilbertiodendron* forest and three 1 ha plots of mixed forest at the Dja Faunal Reserve, Cameroon. Top soil values were calculated by averaging values of the top depth classes: 0–5 cm, 5–10 cm, 10–20 cm and 20–30 cm. Deep soils were 150–200 cm. All values are expressed in mean \pm 95% confidence intervals ($n = 3$). Comparisons of mean values between the monodominant and mixed forests were performed using Wilcoxon signed ranks test for both top soils and deep soils. NS denotes there was non-significant difference between the two forest types ($P > 0.05$).

Parameters	Top soil (0-30 cm)			Deep soil (150-200 cm)		
	Monodominant	Mixed		Monodominant	Mixed	
Proportion of clay (%)	32.6 \pm 7.5	39.1 \pm 10.0	ns	76.8 \pm 13.7	65.1 \pm 24.3	ns
Proportion of silt (%)	49.9 \pm 1.6	47.6 \pm 5.1	ns	14.9 \pm 6.3	29.7 \pm 20.3	ns
Proportion of sand (%)	17.3 \pm 8.1	13.3 \pm 5.8	ns	8.2 \pm 8.8	5.2 \pm 5.5	ns
Median particle size (μm)	12.23 \pm 6.36	8.90 \pm 2.09	ns	3.50 \pm 2.50	5.02 \pm 4.84	ns
Bulk density	0.87 \pm 0.02	1.01 \pm 0.20	ns	1.45 \pm 0.04	1.17 \pm 0.33	ns
pH (H ₂ O)	3.70 \pm 0.09	3.71 \pm 0.04	ns	4.20 \pm 0.14	4.21 \pm 0.18	ns
C (%)	2.03 \pm 0.66	1.89 \pm 0.20	ns	0.32 \pm 0.10	0.37 \pm 0.07	ns
N (%)	0.15 \pm 0.03	0.16 \pm 0.01	ns	0.03 \pm 0.01	0.04 \pm 0.01	ns
C/N	12.31 \pm 1.05	11.45 \pm 0.45	ns	13.06 \pm 5.78	12.26 \pm 3.60	ns
Labile P (ppm)	0.04 \pm 0.01	0.04 \pm 0.01	ns	0.01 \pm 0.00	0.01 \pm 0.01	ns
Inorganic P (ppm)	0.69 \pm 0.29	0.63 \pm 0.18	ns	0.31 \pm 0.12	0.40 \pm 0.20	ns
Total P (ppm)	1.77 \pm 0.26	1.80 \pm 0.45	ns	0.52 \pm 0.12	0.58 \pm 0.10	ns
Al (cmol _e /kg soil)	0.97 \pm 0.17	0.80 \pm 0.10	ns	0.73 \pm 0.18	0.82 \pm 0.30	ns
Ca (cmol _e /kg soil)	0.06 \pm 0.02	0.06 \pm 0.02	ns	0.01 \pm 0.01	0.02 \pm 0.00	ns
K (cmol _e /kg soil)	0.10 \pm 0.02	0.10 \pm 0.02	ns	0.02 \pm 0.00	0.02 \pm 0.00	ns
Mg (cmol _e /kg soil)	0.09 \pm 0.01	0.14 \pm 0.06	ns	0.02 \pm 0.01	0.02 \pm 0.00	ns
Na (cmol _e /kg soil)	0.02 \pm 0.01	0.02 \pm 0.01	ns	0.01 \pm 0.01	0.02 \pm 0.00	ns
Ba (cmol _e /kg soil)	<0.01	<0.01	ns	<0.01	<0.01	ns
Cu (cmol _e /kg soil)	<0.01	<0.01	ns	<0.01	<0.01	ns
Fe (cmol _e /kg soil)	0.23 \pm 0.04	0.29 \pm 0.03	ns	<0.01	<0.01	ns
Mn (cmol _e /kg soil)	<0.01	<0.01	ns	<0.01	<0.01	ns
Ni (cmol _e /kg soil)	<0.01	<0.01	ns	<0.01	<0.01	ns
Si (cmol _e /kg soil)	0.05 \pm 0.02	0.06 \pm 0.01	ns	0.06 \pm 0.01	0.10 \pm 0.01	ns*
Zn (cmol _e /kg soil)	<0.01	<0.01	ns	<0.01	<0.01	ns

*The 95 % confidence intervals of Si concentration at 150–200 cm do not overlap between the two forest types. Nevertheless, Wilcoxon signed ranks test shows that the difference was not significant. The difference is considered non-significant because monodominant forest was not consistently lower in Si concentration along the depth gradient in the top soils when compared with mixed forest (Fig. 2.8).

Figure 2.3 Comparison of soil properties—proportion of clay (A); silt (B); and sand (C)—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values (n = 3) and error bars indicate 95% confidence intervals.

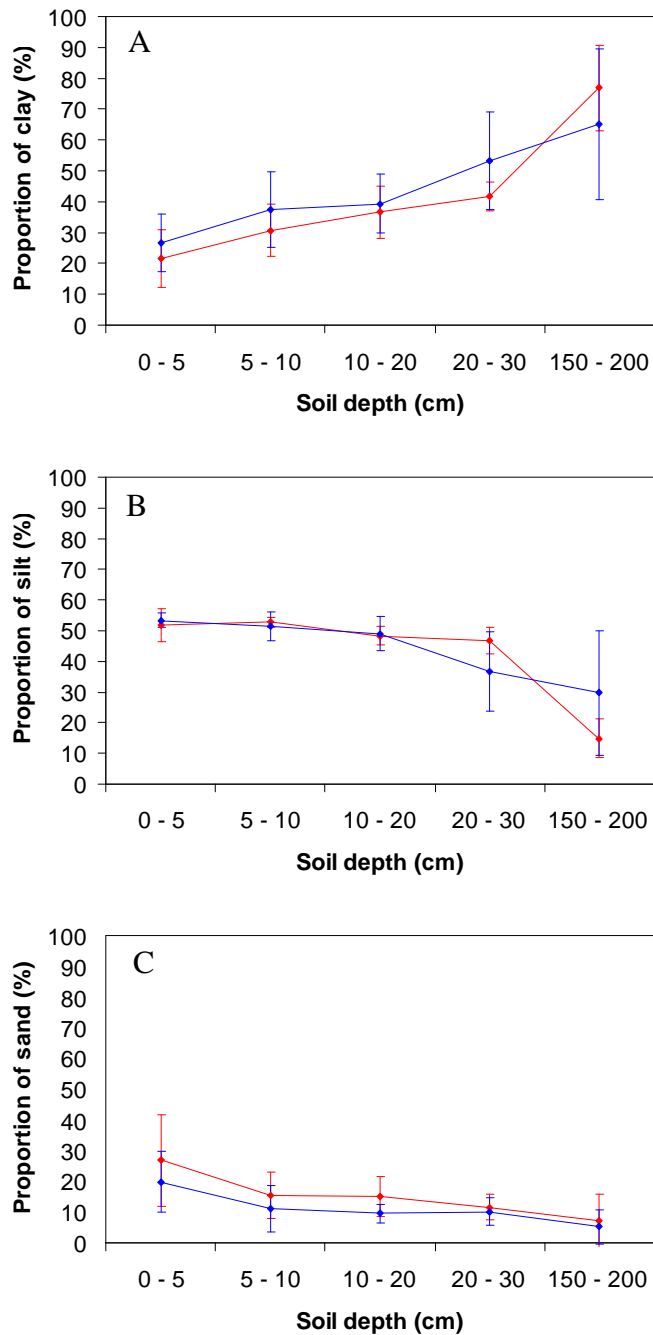


Figure 2.4 Comparison of soil properties—median particle size (A); pH in H₂O (B); and bulk density (C)—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values (n = 3) and error bars indicate 95% confidence intervals.

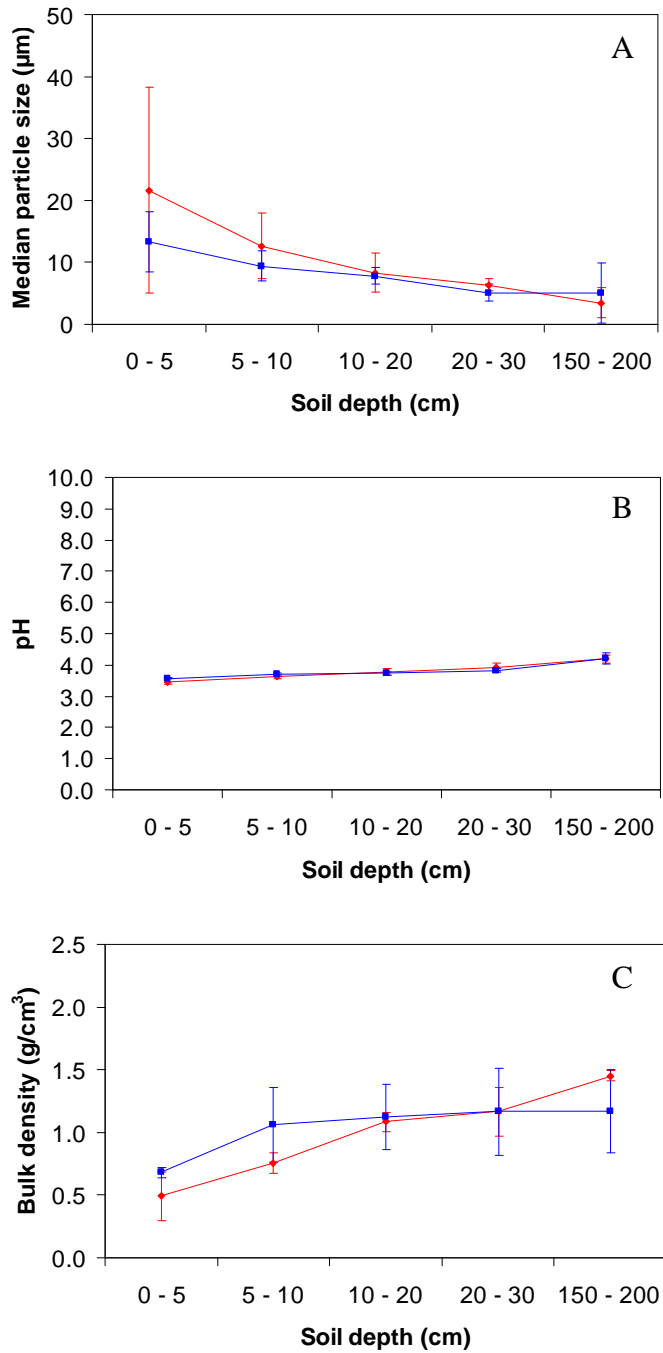


Figure 2.5 Comparison of soil properties—C content of soil organic residues (A); N content of soil organic residues (B); and C/N ratio (C)—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values ($n = 3$) and error bars indicate 95% confidence intervals.

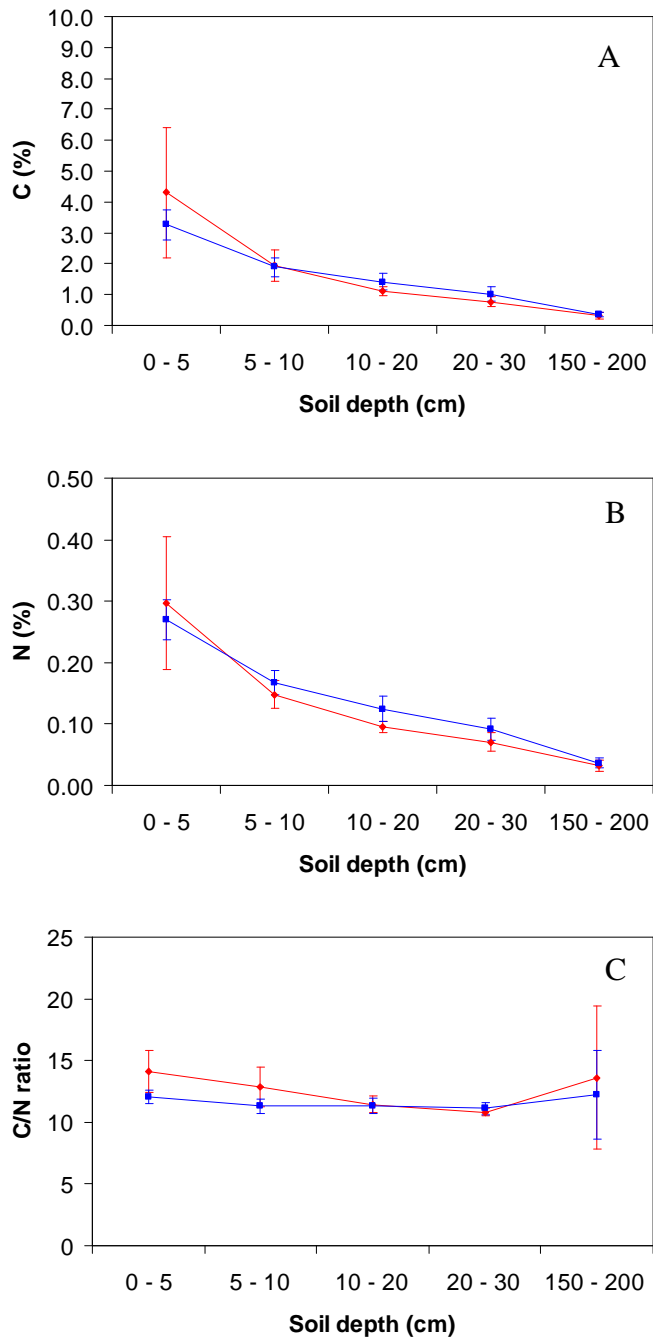


Figure 2.6 Comparison of soil properties—labile P concentration (A); inorganic P concentration (B); and total P concentration (C)—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values ($n = 3$) and error bars indicate 95% confidence intervals.

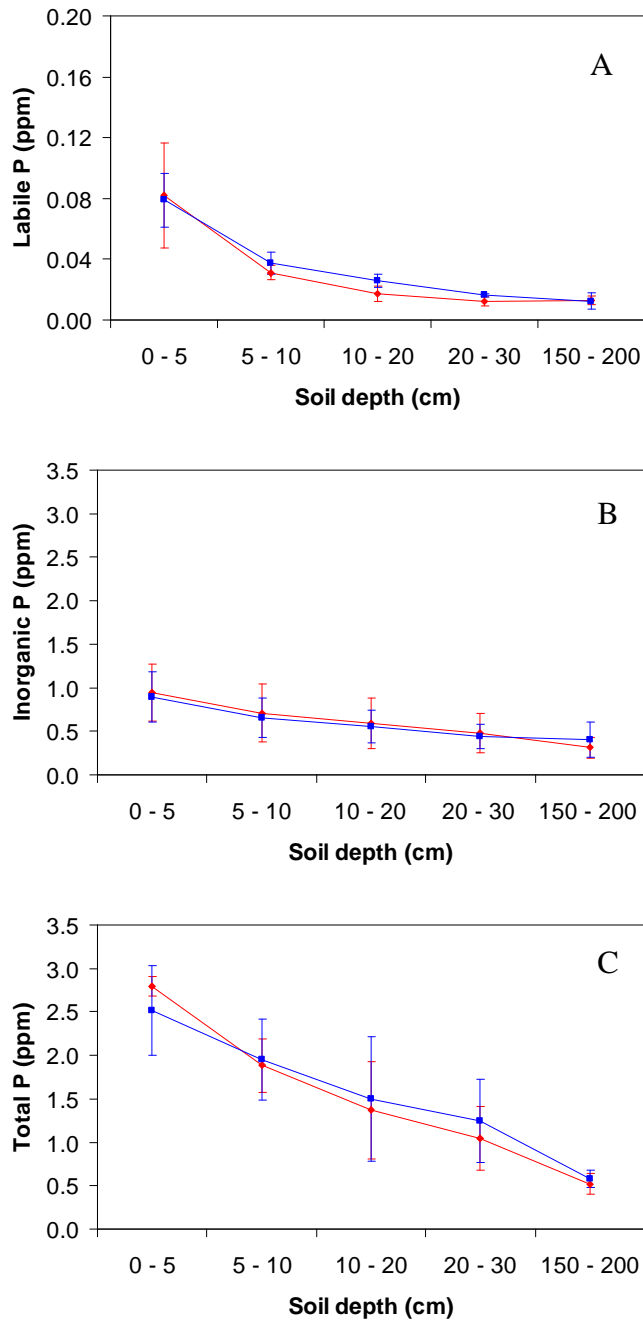


Figure 2.7 Comparison of soil properties—concentrations of Al; Ca; K; Mg; and Na—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values ($n = 3$) and error bars indicate 95% confidence intervals.

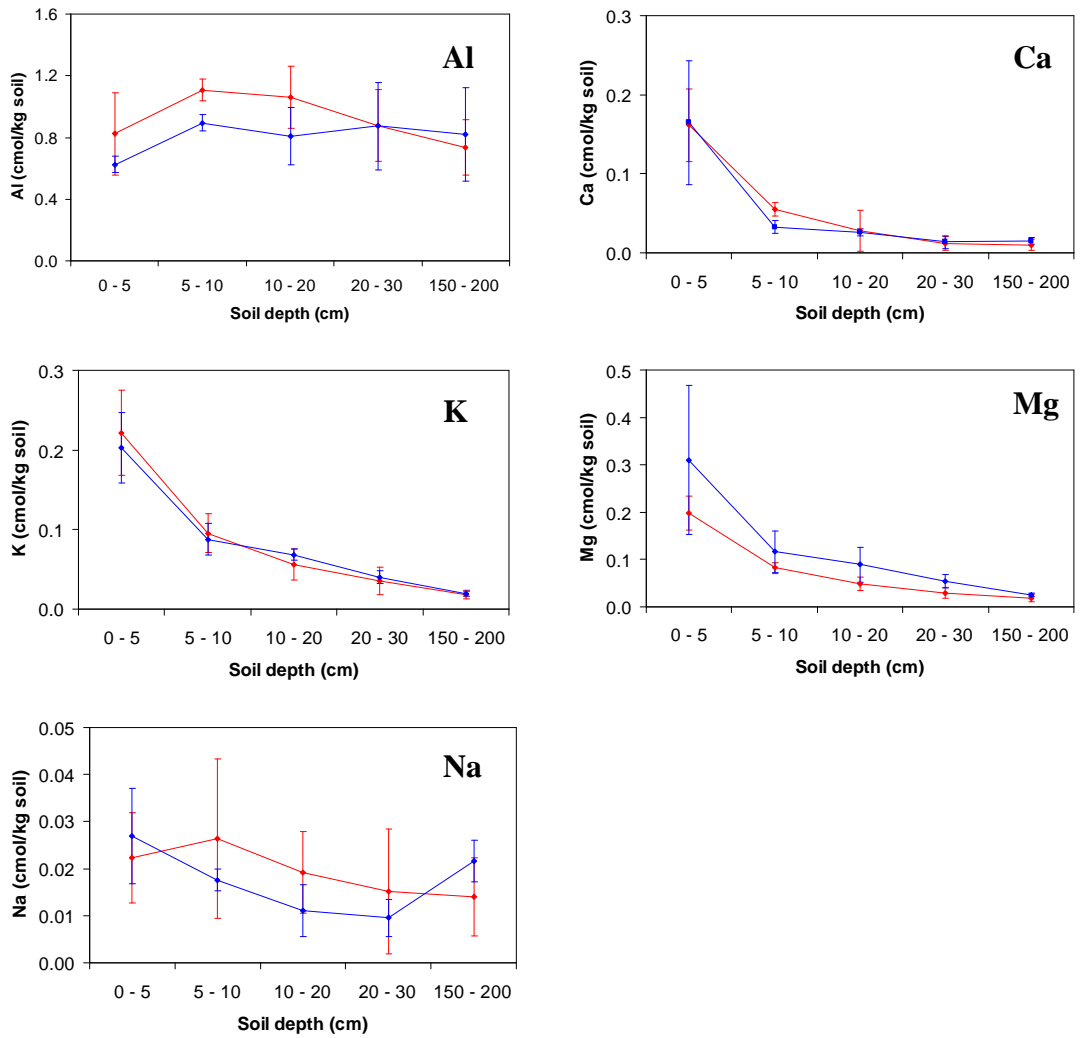
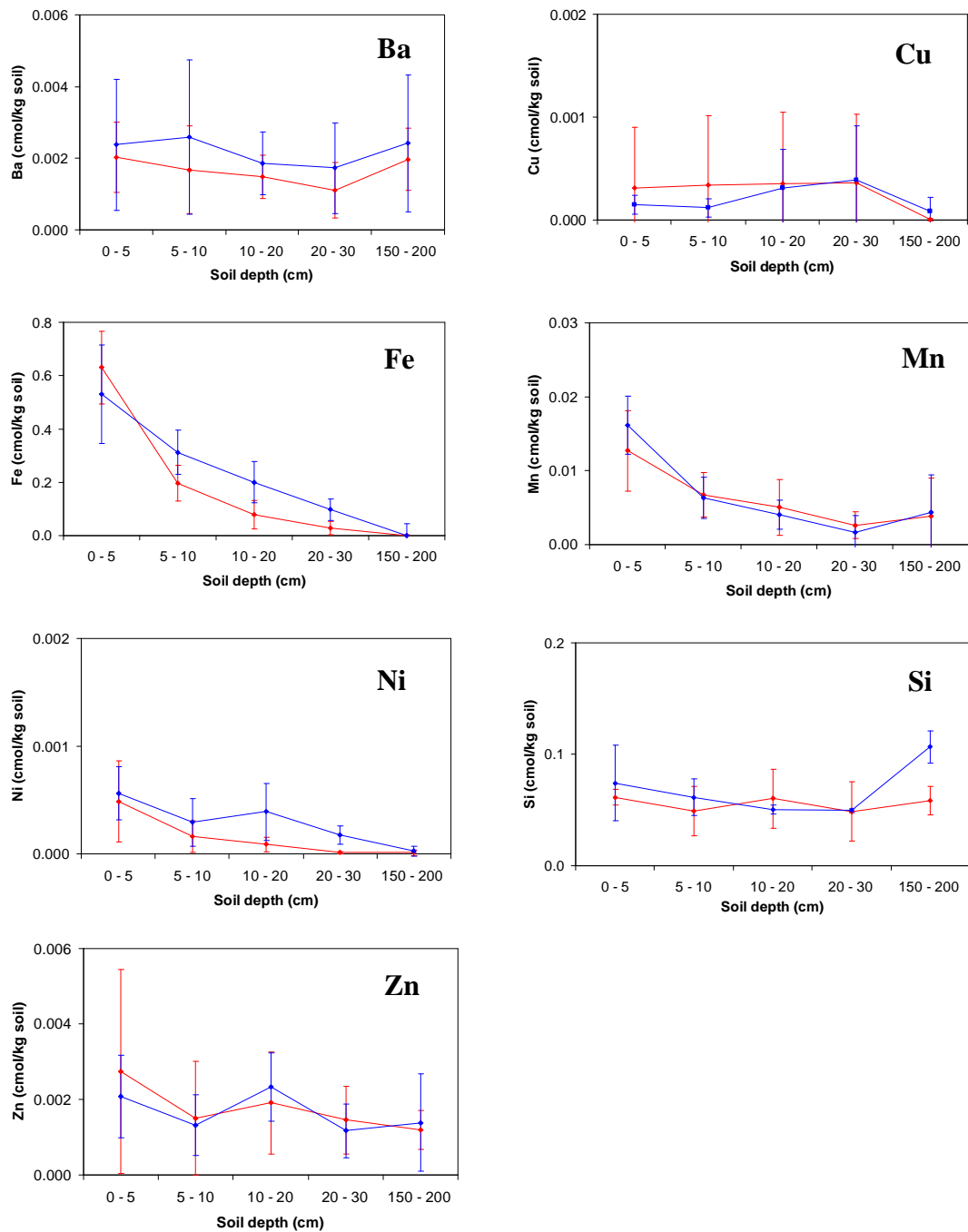


Figure 2.8 Comparison of soil properties—concentrations of Ba; Cu; Fe; Mn; Ni; Si; and Zn—between monodominant *Gilbertiodendron dewevrei* forests (red line) and adjacent mixed forests (blue lines). The dots show mean values (n = 3) and error bars indicate 95% confidence intervals.



For the comparison of Si concentrations in the deep soils between monodominant and mixed forests, the 95 % confidence intervals of Si concentration at 150–200 cm do not overlap between the two forest types. Nevertheless, Wilcoxon signed ranks test shows that the difference was not significant (Table 2.1). I consider the difference non-significant because monodominant forest was not consistently lower in Si concentration along the depth gradient in the top soils when compared with mixed forest (Fig. 2.8).

Generally, soils at depth of 0–5 cm, which are likely to be most influenced by the vegetation, were not different between the monodominant and mixed forests. Analyses at the soil depth of 150–200 cm show that the soils were also not different between the monodominant and mixed forests. I conclude that the edaphic conditions were unlikely to be the cause of monodominance in *G. dewevrei* forests. Although I used a small number of replicate sites in this study, my results are in accordance with those found in *G. dewevrei* forest and its adjacent mixed forest at the Ituri Forest, the Democratic Republic of the Congo (Hart 1985, Hart *et al.* 1989, Conway 1992). Conway (1992) found that there were no differences in the mean values of the soil parameters (pH, organic C, total N, total P, extractable P, total K, total Ca and total Mg) between *G. dewevrei* forests and adjacent mixed forests. Similarly, Hart *et al.* (1989) claimed that “there was no significant difference between mixed forest and *Gilbertiodendron* forest for most soil factors tested”. These soil factors were the concentrations of K, Ca Mg and P in top soils (20-cm depth), and Ca, Mg and P in deep soils (150-cm depth). Although Hart *et al.* (1989) found that the concentrations of K in deep soils between forest types were significantly different, my study and Conway (1994) show that the difference in K concentrations between monodominant and mixed forests was not significant.

However, some differences between the monodominant and mixed forests were recorded at the Ituri Forest by Torti *et al.* (2001). In that study, Torti *et al.* estimated relative availability of N in the two forest types with resin beads (see Torti *et al.* 2001 for details on mixed-bed resin method) and found that the monodominant forests had a lower level (one-third) of N (ammonium and nitrate) availability in the soil than the mixed forests. Such discrepancies

in their findings suggest that we cannot assume all monodominant *Gilbertiodendron* forests have the same soil properties as their adjacent mixed forests.

Low nutrients “could negatively affect the survival of some tree species in the understory of the *Gilbertiodendron* forest” (Torti *et al.* 2001). However, this soil nutrient-related theory on monodominance does not match my empirical observations as this study shows that soils are not the cause of difference in vegetation between the monodominant and mixed forests. Nevertheless, edaphic conditions may be part of a suite of potential positive feedbacks that may lead to a high probability of monodominance being attained (Chapter 1).

2.4. Summary

- There were no significant differences between the monodominant and mixed forests in soil texture, median particle size, bulk density, pH, C content, N content, C/N ratio and concentrations of labile P, inorganic P, total P, Al, Ba, Ca, Cu, Fe, K, Mg, Mn, Na, Ni and Zn.
- Concentrations of Ba, Mg and Ni were consistently, but non-significantly, lower in monodominant than mixed forests, and Si was non-significantly lower at 150–200 cm.
- Little evidence that soil differences determined the locations of *Gilbertiodendron dewevrei* forest.

3. Tree species diversity of monodominant forest in relation to its adjacent mixed forest

3.1. Introduction

Central Africa is recognized for its relatively high plant diversity containing approximately 16000 plant species (Kier *et al.* 2005). Its flora includes a lowland rain forest component in which the communities are highly diverse and complex. However, not all lowland forest communities show a particularly high tree alpha (α -) diversity and these low-diversity forests typify some forested areas in central Africa (e.g., Connell & Lowman 1989; Hart 1985; Hart 1989; Richards 1996; Torti *et al.* 2001). *Gilbertiodendron dewevrei* is a species which often extensively dominates large patches of forests on the plateau in central Africa. These monodominant forests exist alongside higher-diversity forests often with sharp boundaries.

Gilbertiodendron forest involves a large number of *G. dewevrei* co-existing with a number of locally rare species and this might be expected to reduce the α -diversity of species in that area. For example, Hart *et al.* (1989) have shown that “mixed forest (average of 18 species of trees ≥ 10 cm diameter in breast height [dbh] per 25 m \times 25 m plot) is significantly more diverse than *Gilbertiodendron* forest (average of 6 species per plot)”. By contrast, Connell & Lowman (1989) have shown that although the canopy tree diversity negatively correlates with the dominance of *G. dewevrei* within their study plots, “increasing dominance by one canopy species has little effect on the diversity of subcanopy trees”. Similarly, Makana *et al.* (2004a) suggested that the overall number of species within the *Gilbertiodendron* forest over large areas is the same as compared to their adjacent high-diversity forests at the Ituri Forest of the Democratic Republic of the Congo: the α -diversity of tree species (dbh ≥ 1 cm) in a small area (<1 ha) of the *Gilbertiodendron* forest may be reduced because of the dominance of a single species, but “at scales of 1 hectare and above, mixed and monodominant forests had comparable levels of overall species richness among trees ≥ 1 cm dbh”. At a closer examination of data from the presented by Makana *et al.* (2004a), species richness of trees ≥ 10 cm dbh in their 10 ha study plots in *Gilbertiodendron* forest (56 ± 24 species per ha) was also comparable to the 10 ha

plots in adjacent high-diversity forest (68 ± 8 species per ha). In other words, species of the high-diversity forests were not excluded in the *Gilbertiodendron* forests, but they are present at reduced density (Richards 1996).

This chapter addresses the following question: is the species richness of the successfully established non-dominant trees in the *Gilbertiodendron* forest (hereafter called the monodominant forest) the same as its adjacent high-diversity forest (hereafter called the mixed forest) in the Dja Faunal Reserve of south-eastern Cameroon? I defined successfully established tree species to be the ones that have one or more individuals with diameter at breast height (dbh) ≥ 10 cm. Previous comparative studies (e.g., Hart et al. 1989 & Makana *et al.* 2004a) drew different conclusions and therefore the diversity pattern in the monodominant and mixed forests is highly uncertain. This study—for the first time—used species estimators to estimate the true species richness of the two forest types.

This chapter also address the question of whether the successful establishment of non-dominant trees in the monodominant forest is non-random. I compared the life-history attributes of species that were successfully established in the monodominant forest with those that were present in the adjacent mixed forest but were absent in the monodominant forest (i.e., unsuccessful). If life-history traits have an impact on the recruitment of non-dominant species to maturity, I can then (1) conclude that the successful establishment of these species is non-random—i.e., not by chance and (2) identify which subset of the pool of available species successfully invade monodominant forests.

Monodominance in the *Gilbertiodendron* forests has been attributed to the life-history traits of dominant species such as ectomycorrhizal association, being shade tolerant, possessing closed canopy, producing large seeds, and creating deep leaf litter that slowly decomposed (see Chapter 1). Hence, my study demonstrates the utility of comparative studies based on species traits to show if the non-dominant species are able to break through any barriers created by the dominant species and then establish to maturity. This should provide fundamental knowledge for understanding the regeneration processes of the non-dominant species in the monodominant

forests and perhaps assist in elucidating mechanisms that result in monodominance in these forests.

3.2. Method

The study was conducted in the monodominant *Gilbertiodendron* forest and its adjacent mixed forest at the Dja Faunal Reserve (for description of the study area, see Chapter 2). Soils in the two forest types are poorly drained, acidic, silty oxisols (see Chapter 2). Physical and chemical soil properties—soil bulk density, pH, particle size, C and N contents, C/N ratio, concentrations of labile, organic and inorganic P, and other trace elements such as Al, B, Ba, Ca, Co, Cr, Cu, Fe, K, Mn, Mo, Na, Ni, Se, Si, Sr, Ti, V and Zn—along a depth gradient (0–2 m) were not significantly different between the monodominant and mixed forests (for description of soil analyses, see Chapter 2). Hence, the potential differences in diversity were unlikely to be due to edaphic conditions.

3.2.1. Tree sampling

The tree α -diversity in three monodominant *Gilbertiodendron* forests and their adjacent mixed forests were sampled using 100 m \times 100 m (1 ha) plot surveys in February 2005 following the standardized guidelines (Phillips & Baker 2002) by B. Sonké and S. Lewis. In total, six 1 ha plots were surveyed. The three plots in monodominant forest were independent patches chosen based on satellite images and local knowledge. The location of the *Gilbertiodendron* patches was at least 4 km apart from each other. For each *Gilbertiodendron*-dominated plot, a corresponding plot in the adjacent mixed-species forest was established for comparative purposes (For more details of plot establishment, see Chapter 2). Each plot was divided into 20m \times 20m quadrats where species were identified, as far as possible, for all tree stems with dbh \geq 10 cm. Tree was defined as free-standing woody stems. All scientific names for tree taxonomy in this study were standardized for orthography and synonyms with the African Flowering Plant database (<http://www.ville-ge.ch/cjb/bd/africa/index.php>). For unknown species, I collected

voucher specimen for identification at the National Herbarium of Cameroon. I considered species in the monodominant forest to be locally common if there were three or more individuals found within my sampling area of 3 ha, following Hubbell & Foster (1986). To compare the patterns of stem size distribution between the monodominant and mixed forests, I considered for each forest type, the number of stems in different dbh classes (10–20 cm; >20–30 cm; >30–40 cm; >40–50 cm; >50–60 cm; and >60 cm) and the proportion of stems in different dbh classes. In addition, I calculated Fisher's α values for the two forest types.

3.2.2. Tree species traits

To assess which species traits correlate with successful establishment in the monodominant forests, I first compiled a checklist of all species found in the six hectares of forest sampled. I then compared the mixed forest checklist with that of the monodominant forest to identify the list of species that occurred in the plots of both forest types. I restricted my analyses to the 193 positively identified tree species from all study plots.

I compiled ecological trait data that (a) are considered to confer competitive advantages (e.g., Makana *et al.* 2004a; Torti *et al.* 2001), and (b) could be obtained for at least 75% of the 193 species. My analyses focused on the following ecological traits: (1) relative abundance; (2) wood mass density; (3) plant height at maturity; (4) maximum dbh; (5) primary fruit/seed dispersal mechanism; (6) ecological guild in terms of light requirement for seedling establishment; and (7) geographical distribution.

The relative abundance of each species in the mixed forests was based on the three mixed forest plots. I obtained wood mass density, defined as dry wood mass/green wood volume (g cm^{-3}), for each species that occurred in my plots from Lewis *et al.* (2009), which compiled the data from 34 sources (e.g., Bolza & Keating 1972; Rijdsdijk & Laming 1994). Baker *et al.* (2004) showed that the wood density is closely related to phylogeny. Hence I took mean genus-level wood density for individual stems with no species-specific data (34 cases;

17.6 % of 193 species). Stems with genus-level and family-level data not available were classified as cases with missing data (6 cases; 3.1 % of 193 species).

I collected data on other traits for each species based on published literature (e.g., van Gemerden *et al.* 2003; Sonké 2004), herbarium specimens, and personal observations. I classified species according to maximum stature in three classes based on Swaine & Whitmore (1988): large trees (>30 m tall), medium trees (10–30 m tall) and small trees (<10 m tall). I placed species on the basis of maximum dbh in three classes following Sonké (2004): large diameter (>100 cm in dbh), medium diameter (50 cm–100 cm) and small diameter (<50 cm). I ranked each species in one of two categories according to its fruit/seed dispersal mode (biotic and non-biotic dependent). Each species was classified into one of two categories according to its ecological guild in terms of light requirement (pioneer [e.g., light-demanders that require high light level for seedling establishment], and non-pioneer [shade-bearers that are capable of seedling establishment under forest shade, though some shade-bearers may need higher light level at later stage of life]), and each was grouped according to its geographical distribution (narrow, i.e., species endemic to lower-Guinea-Congolean biogeographical region; and wide that includes species which were not endemic to the region).

3.2.3. Species richness estimations

I graphed sample-based rarefaction curves (i.e., equivalent to smoothed accumulation curves) rescaled to (i) the number of individuals to compare the number of tree species between the different forest types, and (ii) the number of samples (i.e., quadrats) to compare the density of forest species between these forest types. I then plotted curves of the number of individuals against the number of samples to compare the population density. Further, for statistical corroboration of potential differences in forest species richness between the monodominant and mixed forest, I compared the mean number of tree species per quadrat between forest types.

Because rarefaction cannot be used for extrapolation from smaller samples, it does not provide an estimate of asymptotic species richness (Gotelli & Colwell 2001). To estimate the

tree species richness for each forest type, I generated non-parametric species estimators from EstimateS (Colwell 2005) based on the distribution of rare species in the community assemblage of each forest type (Colwell & Coddington 1994). I used nine different nonparametric species estimators: ACE (abundance-based coverage estimator), ICE (incidence-based coverage estimator), Chao1, Chao2, Jackknife1, Jackknife2, Michaelis-Menten, and bootstrap methods, because different estimators perform best for different data sets (Walther & Morand 1998).

3.2.4. Statistical analyses of establishment

To examine the effects of individual species traits on the recruitment to maturity in the monodominant forest, I performed two-variable binomial logistic regressions (logit model) between each trait and the status of each non-dominant tree species in the monodominant forest, categorized as presence (successful) or absent (unsuccessful). My data precluded the use of the independent-contrasts approach (Purvis *et al.* 2000) for controlling the effects of phylogenetic autocorrelations because of the inclusion of categorical variables (e.g., primary fruit/seed dispersal mechanism) in my analyses and the lack of complete phylogeny of the study taxa (O. Hardy, pers. comm.). As an alternative, I included family as a covariate in my statistical analyses. For families consist of less than 10 species in my sample, I lumped them as one single family to prevent problem of low 'cell count' that may result in the regression not reaching convergence for parameter estimate (Menard 2002). Any phylogenetic effect at the genus level is likely to be poorly represented because most genera in my data set are species poor with only 1.54 species per genus on average and 70% of species do not have congeners. To assess the influence of phylogeny on the analyses, I repeated the same tests with each species trait as the sole independent variable without family as a covariate. These analyses allow unequal sample sizes for all variables (i.e., missing data). Nevertheless, the sample size for each variable was large ($n \geq 144$ species; at least 75 % of the 193 species complete for each variable).

To determine the most parsimonious model that predicts successful establishment, I used Akaike's Information Criteria (AIC) to find the model that has the best combination of significant life-history variables retained by the univariate analyses. However, I did not test all the possible permutations of all significant variables in order to keep the number of candidate models to the minimum (see Anderson & Burnham 2002). Models that comprised only a single variable were excluded in the analysis because the establishment success is unlikely to be accounted for by only one variable. Since my sample size was relatively small, I employed the second-order model selection criterion AIC_c , which is a small sample bias-corrected version of AIC (see Burnham & Anderson 1998). For a model M_i , AIC_c is expressed as:

$$AIC_c = -2 \times \log(\text{likelihood}) + 2K + (2K[K + 1]) / (n - K - 1)$$

where $\log(\text{likelihood})$ is the log-transformed value of the likelihood, K is the number of parameters, and n is the sample size (Burnham & Anderson 2002).

The best candidate model was identified by its lowest AIC difference and highest Akaike weight (see Burnham & Anderson 2002) and its variables were used to construct a multiple logistic regression model for predicting the successful establishment of a tree species in the monodominant forest. As the regression analysis is based on the assumption that the predictor variables are linearly independent of each other, I used the principal components analysis (PCA) to check for multicollinearity among the variables (Chatterjee *et al.* 2000). A measure of the overall multicollinearity of the variables was obtained by calculating the condition number (κ) which is defined by $\kappa = \sqrt{\lambda_1 / \lambda_p}$ where λ_1 is the maximum eigenvalue of the correlation matrix and λ_p is the minimum eigenvalue of the correlation matrix. Collinearity is deemed to be a problem if value of $\kappa > 15$. All statistical analyses were performed using Minitab (version 14) and SPSS (version 14.0) statistical software.

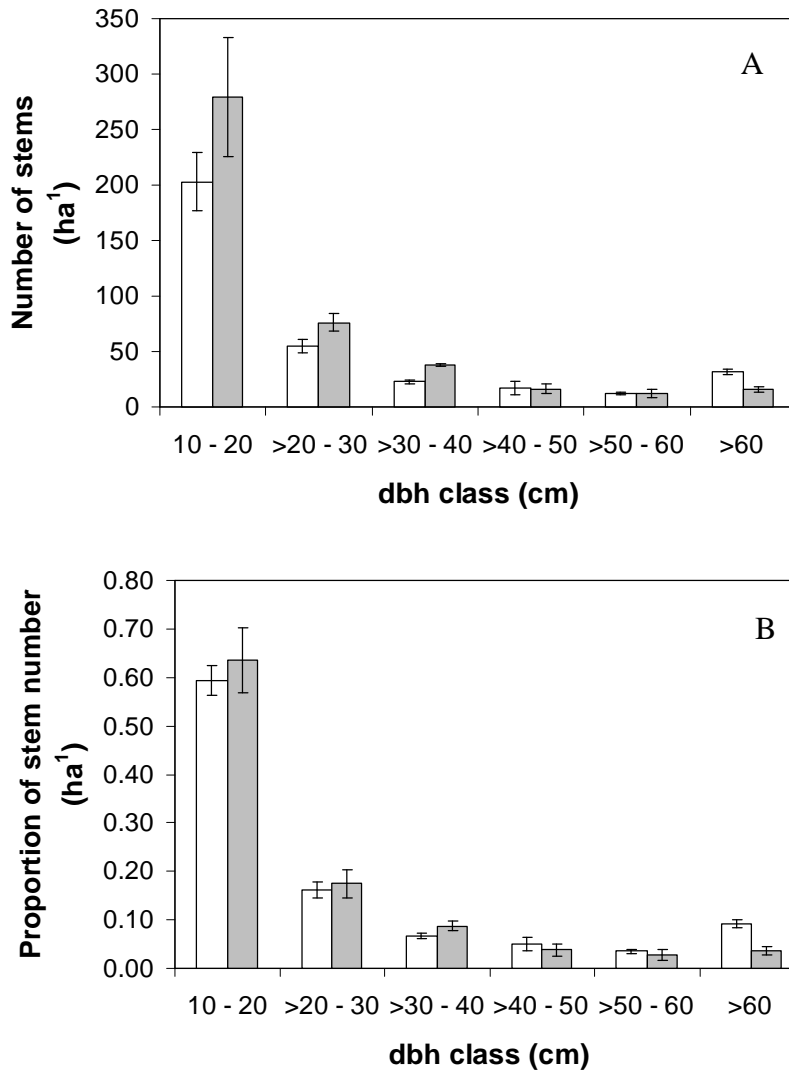
3.3. Results

3.3.1. Comparing monodominant and mixed forest diversity

In the 6 ha, I recorded a total of 2336 individual stems representing 211 identified tree species and morphotypes (194 species, 17 morphotypes; Appendix A). In the monodominant forest plots of 3 ha, there were 71 tree species and morphotypes recorded (including *G. dewevrei*). Ten tree species in the monodominant plots were not recorded in the mixed forest plots (Appendix A), although they do occur in mixed forest outside my plots (Sonké 2004). Only two stems in the monodominant forests were treated as morphotypes. In the mixed forest plots of 3 ha, 183 tree species were recorded and 15 stems were considered as morphotypes. There were 125 tree species (excluding morphotypes) unique to the mixed habitat (i.e. not found in the monodominant forest plots).

Most of the individual stems with dbh ≥ 10 cm were in the dbh class of 10–20 cm for both forest types (Fig. 3.1). Both forest systems had their number of stems decreased with increasing size classes (Fig. 3.1). However, the mixed forests had significantly more trees of dbh >20–30 cm and >30–40 cm, and fewer larger trees of dbh >60 cm than the monodominant forests (Fig. 3.1A). The proportion of trees in different dbh classes was not significantly different between the two forest types, except that monodominant forests had a greater proportion of trees of dbh >60 cm and lower proportion of trees of dbh >30–40 cm (Fig. 3.1B).

Figure 3.1 Allocation of number of stems (A) and proportion of stem number (B) in different diameter in breast height (dbh) classes in monodominant *Gilbertiodendron* forests (white bars) and mixed forests (grey bars). Error bars represent 95% confidence intervals.



The monodominant forest had lower estimated species diversity values than the mixed forest (Table 3.1). The mean forest tree species richness estimates (\pm 95% confidence interval) from the nine estimators were 114.28 ± 11.49 for the monodominant forest and 305.24 ± 41.63 for mixed forest. The mean number of forest species recorded per quadrat (i.e., species density) among the vegetation types were 3.73 ± 0.40 and 13.97 ± 0.82 for the monodominant forest and the mixed forest, respectively. The mean number of individuals observed per quadrat (i.e., stem density) for the monodominant forest was 13.68 ± 0.82 and that for the mixed forest was 17.47 ± 0.92 . The rarefaction curves suggested that the monodominant forest had lower tree species richness, tree species density, and population density compared to the mixed forest (Fig. 3.2, A–C). In addition, the monodominant forest had lower Fisher's α value than the mixed forest (Table 3.1).

3.3.2. Life-history traits

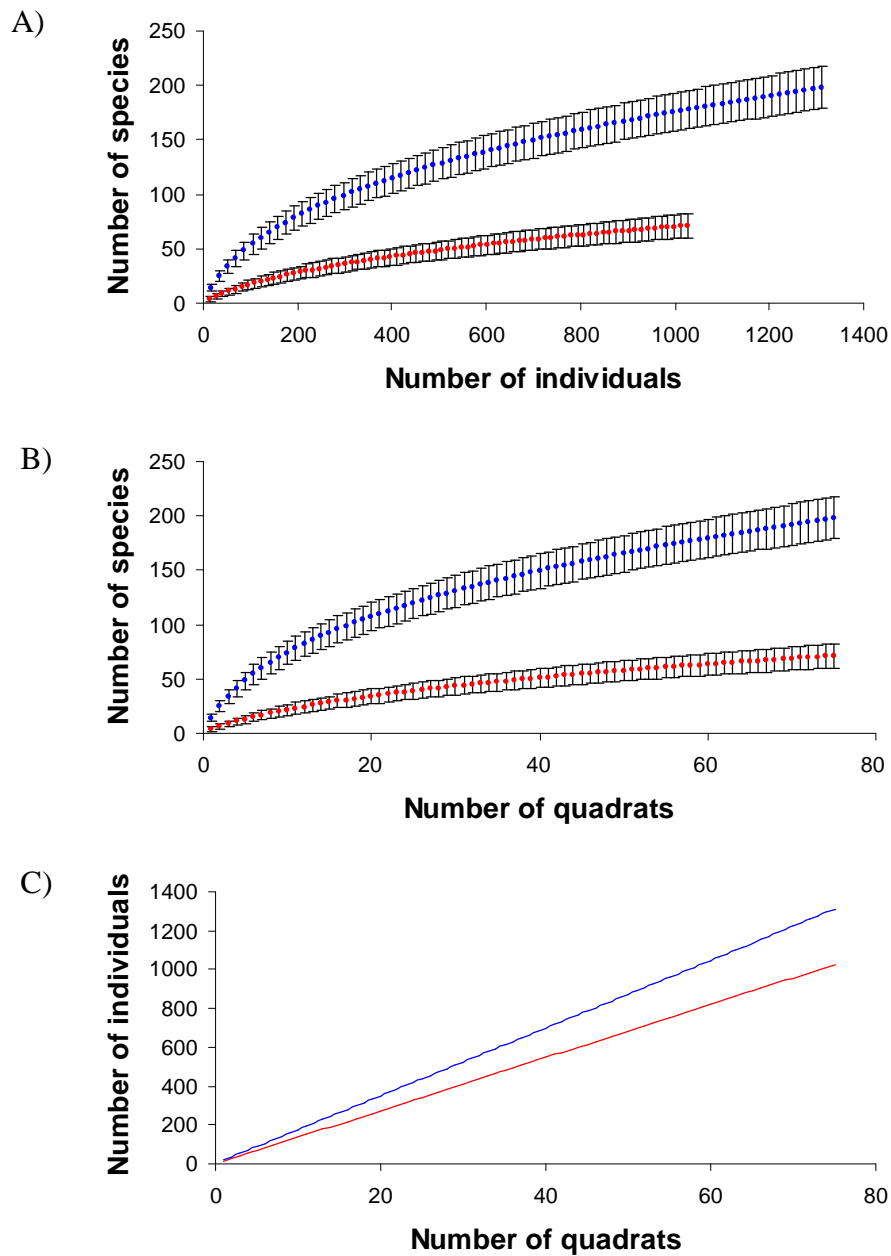
I recorded 198 tree species and morphotypes in the mixed forests of which only 58 species (29.3%) were recorded in the monodominant forests. These non-dominant species in the monodominant systems were represented by 192 individual stems (18.9% of individual stems recorded in the three monodominant forest plots). At the species level, 23 (35%) non-dominant species in the monodominant forest were considered to be locally common (≥ 1 stem ha^{-1}) and 41 species to be rare (< 1 stem ha^{-1}) (Appendix A). Only eight common non-dominant species in the monodominant forest had 10 or more individuals recorded within the three 1 ha plots (i.e., ≥ 3.3 stems ha^{-1}): *Angylocalyx pynaerthii* (5.0 stems ha^{-1}); *Carapa procera* (4.7 stems ha^{-1}); *Desbordesia glaucescens* (4.3 stems ha^{-1}); *Staudtia stipitata* (4.0 stems ha^{-1}); *Pentaclethra macrophylal* (3.7 stems ha^{-1}); *Strombosia pustulata* (3.7 stems ha^{-1}); *Trichoscypha acuminata* (3.7 stems ha^{-1}); and *Mammea africana* (3.3 stems ha^{-1}).

Table 3.1 Nonparametric species richness estimations and Fisher's α values of the monodominant *Gilbertiodendron* forest and the adjacent mixed forest.

Parameters*	Monodominant forest		Mixed forest	
n	75		75	
Sp _{obs}	71		198	
Ind _{obs}	1026		1310	
ACE	125.85	(0.56)	324.48	(0.61)
ICE	133.91	(0.53)	332.42	(0.60)
Chao1	119.17	(0.60)	380.29	(0.52)
Chao2	129.91	(0.55)	381.99	(0.52)
Jack1	106.52	(0.67)	285.81	(0.69)
Jack2	131.00	(0.54)	353.24	(0.56)
Bootstrap	86.10	(0.82)	234.38	(0.84)
MMRuns	101.68	(0.70)	226.84	(0.87)
MMMean	94.42	(0.75)	227.74	(0.87)
Mean \pm 95% confidence interval	114.28	\pm 11.49	305.24	\pm 41.63
Fisher's α	10.02	\pm 0.96	49.99	\pm 9.02

* A total of 211 tree species and morphotypes were recorded from plot surveys (a total of 3 ha for each forest type). n represents sample size (number of 20 m \times 20 m quadrats); Sp_{obs} and Ind_{obs} represent total number of species and individuals observed, respectively. ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans are nonparametric species estimators. Number in parentheses represents the proportion of the estimated species richness that was observed.

Figure 3.2 Sample-based rarefaction curves of the tree communities found in monodominant *Gilbertiodendron* forests (red dots and line) and mixed forests (blue dots and line) comparing number of species (A), species density (B) and population density (C). Error bars represent 95% confidence interval.



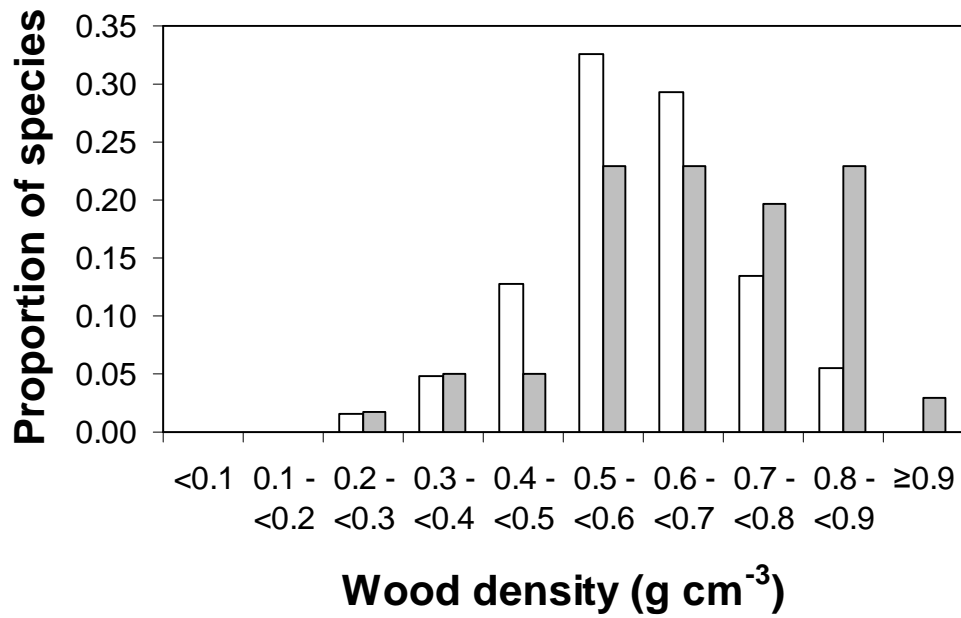
The univariate analysis results indicated that high wood density, high relative abundance in adjacent mixed forest and low light tolerance were significant ($P < 0.05$) determinants of non-dominant tree species that were successfully established in monodominant forest (Table 3.2). Similar results were obtained when the regressions were repeated having each trait as the sole independent variable without family as a covariate. Among these traits, relative abundance in mixed forest ($P < 0.001$) was the most important correlate of tree species success likelihood in establishment in the monodominant forest. The mean abundance (\pm 95% confidence intervals) of the species that successfully established in monodominant forest, in the mixed plots was 4.2 ± 1.5 individuals ha^{-1} . This was significantly different from that of the species in mixed forest plots that were absent in monodominant forest plots (1.1 ± 0.3 individuals ha^{-1}).

The mean wood density of all the non-dominant species in the monodominant forest plots was 0.659 ± 0.038 g cm^{-3} and was significantly different from that of the species in the mixed forest plots that were not found in the monodominant forest plots (0.598 ± 0.021 g cm^{-3}). There is an association between species of certain wood density categories and successful establishment in the monodominant forest (Fig. 3.3). In particular, the species with wood density > 0.79 g cm^{-3} were more likely to be established in the monodominant forest ($\chi^2 = 15.19$, d.f. = 4, $P < 0.01$). There were only three species (2%) among the non-dominant species in the monodominant forest plots that were pioneer (i.e., incapable of seedling establishment under the forest shade), whereas 13% of the species found exclusively in the mixed forest plots were pioneers.

Table 3.2 Relationship between traits of tree species and their occurrence in monodominant *Gilbertiodendron* forests. $P < 0.001$ is denoted by ** and $P < 0.05$ by *.

Variable	n	As sole variable			With family		
		coefficient	<i>P</i>	odds ratio	coefficient	<i>P</i>	odds ratio
Relative abundance	193	0.10	<0.001	1.11 **	0.10	<0.001	1.11 **
Wood density	187	3.57	0.004	35.61 *	3.78	0.004	43.92 *
Height	148						
medium		0.50	0.365	1.65	0.39	0.496	1.47
tall		0.52	0.361	1.68	0.33	0.578	1.39
Diameter at breast height	146						
medium		-0.07	0.879	0.93	-0.18	0.698	0.83
large		0.59	0.131	1.80	0.45	0.283	1.57
Light requirement	145						
shade tolerance		1.86	0.004	6.44 *	1.82	0.006	6.18 *
Geographical distribution	144						
wide		-0.33	0.656	0.72	-0.42	0.586	0.66
Family	192						
Legumes		0.38	0.449	1.46			
Amnonaceae		0.29	0.619	1.33			
Euphorbiaceae		-0.61	0.200	0.54			
Meliaceae		0.98	0.148	2.67			
Rubiaceae		-1.62	0.131	0.20			
Sapotaceae		-0.12	0.873	0.89			

Figure 3.3 The association of wood density categories and successful establishment of species in the monodominant *Gilbertiodendron* forest. The white bars represent the species absent in the monodominant forest and the grey bars represent those present in the monodominant forest.



There was little evidence of multicollinearity ($k = 1.46$) between the three variables retained from the univariate-regression analyses (i.e., relative abundance, wood mass density and light requirement). The first and second axes of principal component analysis (PCA) matrix represented 45.1% and 33.6% of the variance in my data, respectively, where both axes were the gradients of wood density, relative abundance and light requirement (Fig. 3.4). A principal component ordination of tree species over the three variables did not clearly distinguish species that were present or absent in the monodominant forest, although there appeared to be a concentration of species that occurred in the monodominant forest in the right hand quadrant of the principal component space (Fig. 3.4). Among these species, one group representing species of higher wood density clustered in the lower right quadrant whereas another associated with greater relative abundance in mixed forest clustered in the upper right quadrant.

If the global model (i.e., one that includes all variables retained by the univariate analyses) adequately described the data, AIC_c could select a parsimonious model that fits (Anderson & Burnham, 2002). To determine whether the global model had a good fit, I performed the Hosmer-Lemeshow goodness-of-fit test on the global model and the test statistics showed that my global model adequately fitted the data ($\chi^2 = 9.38$, $df = 8$, $P > 0.05$). Of the four candidate models generated, based on the permutations of significant variables retained by the univariate analyses, the most parsimonious model selected by AIC_c was the one that includes wood density, relative abundance and light requirement (Table 3.3). This model was at least 49 times more strongly supported by the data than the other simpler variant models (Table 3.3).

Figure 3.4 Ordination of tree species in the principal components space of wood density, light requirement and relative abundance. PC1 and PC2 represent axis 1 and axis 2 of the principal component analysis, respectively. The black dots represent the tree species that were found in the mixed forest plots only. The red squares represent those that were established (i.e., dbh ≥ 10 cm) in monodominant *Gilbertiodendron* forests. The numbers denote the positions of some species: 1, *Musanga ceropioides*; 2, *Ceiba pentandra*; 3, *Alstonia boonei*; 4, *Macaranga spinosa*; 5, *Macaranga grandis*; 6, *Myrianthus arboreus*; 7, *Tabernaemontana crassa*; 8, *Anonidium mannii*; 9, *Carapa procera*; 10, *Polyalthia suaveolens*; 11, *Petersianthus macrocarpus*; 12, *Pentaclethra macrophylla*; 13, *Uapaca paluosa*; 14, *Desbordesia glaucescens*; and 15, *Klainedoxa gabonensis*.

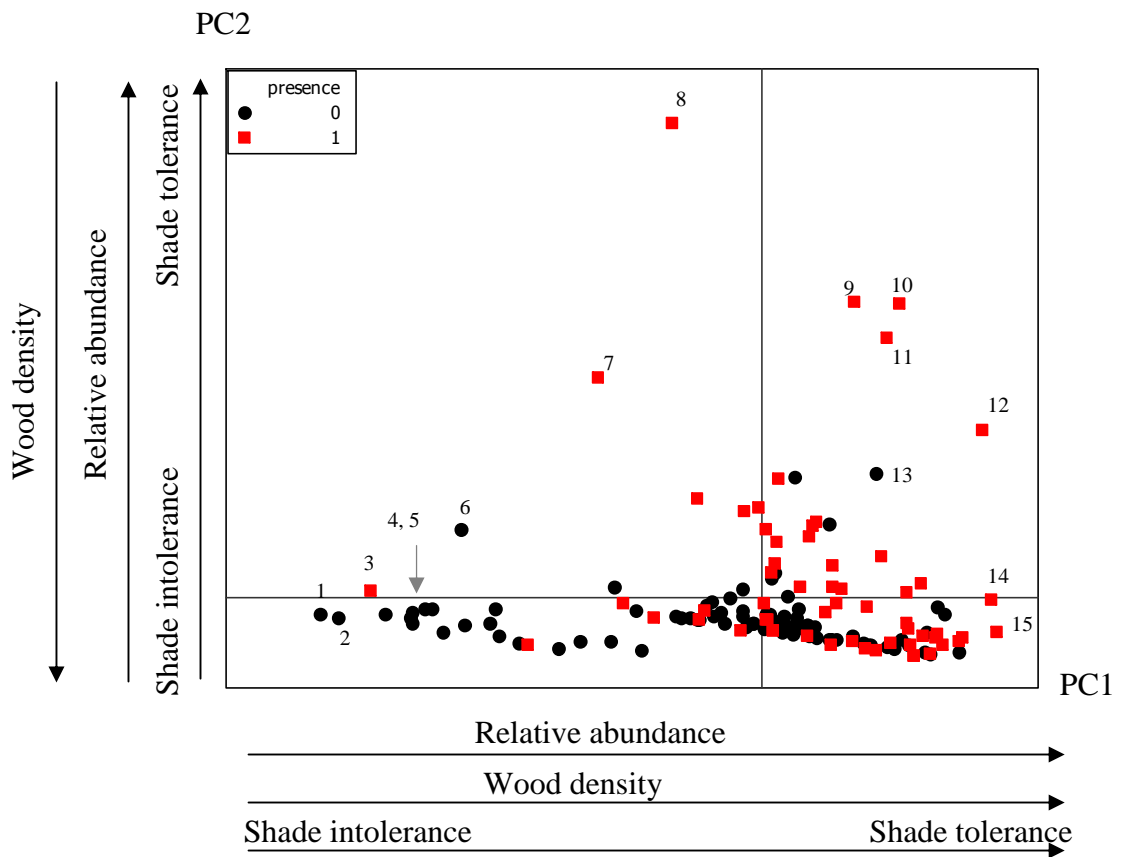


Table 3.3 Binary regression models for establishment success of non-dominant tree species in monodominant *Gilbertiodendron* forest at Dja Faunal Reserve with corresponding log-likelihood, number of parameter (K), Akaike's information Criterion (AIC_c) score and Akaike parameter weight (w_p). ΔAIC_c indicates the difference between each model and the best model (lowest ΔAIC_c ; rank 1). Data include 145 tree species sampled in all monodominant and mixed forest plots. Abundance, density and shade refer to life-history variables: abundance, number of individuals found in the mixed forest plots; density, wood density; and shade, light requirement for seedling establishment. Models are ranked by ΔAIC_c and w_p . The best model that has $\Delta AIC_c < 1$ is bolded.

Rank	Model	r	log-likelihood	K	AICc	ΔAIC_c	w_p
1	abundance \times density \times shade	0.217	-79.190	4	166.66	0.00	0.98
2	abundance \times shade	0.195	-84.038	3	174.25	7.58	0.02
3	density \times shade	0.105	-88.441	3	183.05	16.39	0.00
4	abundance \times density	0.189	-101.181	3	208.53	41.87	0.00

Thus, in this final model, species from the mixed forest with higher wood density and relative abundance, and lower light requirement had a higher probability of establishment in the monodominant forest. The coefficient and odds ratio for wood density (Table 3.4) express the effect of an increase of 1 g cm^{-3} in wood density when the other variables in the analyses remain unchanged. However, it is more meaningful if a more realistic specific wood density difference is stated. Thus, for an increment of 0.1 g cm^{-3} , the coefficient 3.03 (Table 3.4) may be multiplied by 0.1 to obtain 0.30 which is the natural log of 1.35 (odds ratio). In other words, for every 0.1 g cm^{-3} , the odds of achieving establishment improve by 1.35. For a given wood density and relative abundance in the adjacent mixed forest, non-pioneer species of lower light requirement were 5.1 times more likely to establish in the monodominant forests than species that are light demanding (Table 3.4). Finally, for a given light requirement and wood density, an increment of 1 individual in a 3 ha mixed forest improves the odds of the species achieving establishment in a 3 ha monodominant forest by 1.09 (Table 3.4).

Table 3.4 Final multiple logistic regression model explaining the establishment of non-dominant tree species in the monodominant *Gilbertiodendron* forest.

Parameter	Coefficient	<i>P</i>	odds ratio
Constant	-4.10	<0.001	
relative abundance	0.08	0.002	1.09
wood density	3.03	0.033	20.67
light requirement shade tolerance	1.63	0.033	5.11

* Model concordance = 74.3%; n = 140.

3.4. Discussion

In south-eastern Cameroon, I compared species richness among the trees with stem diameters ≥ 10 cm in monodominant *Gilbertiodendron* forest, to that of the adjacent mixed forest. Based on taxon sampling curves, my results provide evidence that the monodominant forest has lower species richness, species density and population density than the adjacent mixed forest.

For each forest type, I calculated Fisher's α value for comparison purposes with the other African (Makana *et al.* 2004; Parmentier *et al.* 2007) and Neotropical forest plots (Johnston & Gillman 1995; Parmentier *et al.* 2007). Mean Fisher's α values (\pm 95% confidence interval, $n = 3$) of trees with dbh ≥ 10 cm, for the monodominant and mixed plots in this study were 10.02 ± 0.96 and 49.99 ± 9.02 , respectively. Fisher's α of trees with dbh ≥ 10 cm in my mixed forest plots (1 ha) was higher than that of mixed forest plots (Fisher's α : 19.5 and 21.9 per hectare based on two 10 ha plots) at Ituri Forest in the Democratic Republic of the Congo (Manaka *et al.* 2004b), but within the range recorded for a typical African mixed forest (mean Fisher's α : 40.4 ± 13.8 , Parmentier *et al.* 2007). On the global level, my mixed forest plots (1 ha) were less diverse as compared to the 1 ha plots in Neotropics (mean Fisher's α : 74.6 ± 45.0 ; Parmentier *et al.* 2007). Although it is not surprising that my monodominant forest plots (1 ha) had lower species diversity than the mixed plots in Africa and the Neotropics, they were also less diverse as compared to the monodominant *Gilbertiodendron* plots at Ituri Forest (Fisher's α based on trees with dbh ≥ 10 cm: 15.3 and 20.2 per hectare based on two 10 ha plots; Manaka *et al.* 2004b). Further comparisons with studies of other monodominant forests are restricted by limited sampling efforts and the data reported (also see Read *et al.* 2000).

There are only a handful of monodominant forest sites whereby their tree species diversity was compared to the adjacent mixed forests (e.g., *Gilbertiodendron* forests at Ituri: Hart *et al.* 1989, Makana *et al.* 2004a; *Nothofagus* forests in New Caledonia: Read *et al.* 2000). Although lower species richness in the monodominant forest shown in my study is in accordance with some studies (Hart *et al.* 1989; Read *et al.* 2000), my results are in contradiction to those of Makana *et al.* (2004b). At Ituri forest plots, Makana *et al.* (2004b)

found that species richness, based on stem size ≥ 10 cm in sampling areas of 1 ha, was comparable in the monodominant and mixed forests. They suggested that most of the richness in monodominant forest is accounted for either by rare species or by species with highly clumped distributions (i.e., high patchiness). However, my results provide evidence that the *Gilbertiodendron* forests had lower species richness, species density and population density than its adjacent mixed forests in terms of established trees of dbh ≥ 10 cm. The asymptotic smoothed species accumulation curves for the monodominant and mixed forests indicate that these forests were generally adequately sampled. My species estimators suggest the same level of completeness for my species inventories within the monodominant forest (53–82% of estimated species detected) and mixed forest (52–87%).

Admittedly, the total sampling area for each forest type in this study was only 3 ha. However, I compared the species richness between the two forest types based on taxon sampling curves that accounts for (1) differences in sampling effort (e.g., number of stems measured) between the forest types and (2) natural levels of sample heterogeneity (i.e., patchiness) in the data (Gotelli & Colwell 2001). Additionally, all the nine nonparametric species estimators unanimously showed that the monodominant forests have lower estimated true species richness. The discrepancy of my findings with those of Makana *et al.* (2004a) suggest that there may be a regional variation in species richness among the *Gilbertiodendron* forests, and the association of high species richness with monodominance remains inconclusive and equivocal. On the other hand, the conflicting results of Makana *et al.* (2004a) could be due to their inclusion of 2.5 ha of mixed forest in one of their 10 ha monodominant plots (Makana *et al.* 2004b). Furthermore, one of their mixed forest plots contained monodominant patches (Makana *et al.* 2004b). Nevertheless, the studies at Ituri Forest plots (Makana *et al.* 2004a, b) showed a high diversity of trees and shrub < 10 cm dbh in both forest types.

In this study, I evaluated each life history traits to identify important determinants for the non-dominant species to establish and attain maturity (i.e., dbh ≥ 10 cm) in the monodominant forest. It has been hypothesized that shorter tree species that are able to complete their life cycles under the shade will be more represented in the monodominant stands

(e.g., Makana *et al.* 2004). Similarly, trees with small maximum dbh size (i.e., slender species) will be able to grow in height at a faster rate (Poorter *et al.* 2003) and to have better access to light in the closing canopy (Poorter *et al.* 2005) than those with larger stems, and thus less affected by the dominance of *Gilbertiodendron*. However, tree height at maturity was not a significant determinant of establishment probability in the monodominant stands nor was maximum dbh.

More widely distributed species may be better able to exploit a wide range of ecological niches than species with narrow distributions (Jablonski 1991). Although geographical distribution may be an indication of the ability to tolerate different environmental conditions across a wide range of taxonomic groups (e.g., primates, Harcourt *et al.* 2002; birds, Jones *et al.* 2001), species with wide geographical distribution size was not a significant positive determinant of successful establishment in the monodominant forests. My results suggest that the more widely distributed species are not inherently more adapted to the monodominant forests.

Tree species in mixed forests that are dependent on biotic agents could enhance the beneficial dispersal of their seeds through reliable disperser visitation to maximize the chances for their seed to be deposited in the monodominant forests. This is on the basis that many of the seed dispersal agents (e.g., primates and hornbills) have large home ranges, thus the probability of their seeds being transported to the monodominant forests is increased. In this study, the biotic dependent dispersal mode had no significant effect on the tree species establishment in the monodominant forests. Instead, approximately 15% of the common non-dominant species (i.e., at least one individual per ha) in the monodominant forests were dependent on wind, explosive mechanism or no obvious adaptation. This may be explained by the fact that the monodominant forests often occur adjacent to mixed forests: the juxtaposition of the two distinct forest types does not necessarily require the non-dominating species to rely on long-ranging animal dispersers to increase their probability of establishment in monodominant forests.

My results indicate evidence for the importance of relative abundance in mixed forests for the occurrence of mature individuals in the monodominant forests. The presence of a greater number of individuals in mixed forests significantly increased the establishment success of tree species in the adjacent monodominant forests. Species' relative abundance in the mixed forests was important for their establishment in the adjacent monodominant forests for two possible reasons. First, probability of establishment in the monodominant forests is dependent on the number of propagules released, which in turn depends on the number of individuals in the nearby mixed forests. Success rate for establishment may increase as more propagules are released. Second, more individuals in the mixed forests means that repeated attempts could occur before the species successfully established themselves. An analogy is the classic case of introduction success in exotic New Zealand birds with larger initial population size (Veltman *et al.* 1996). Relative abundance that significantly influenced the successful establishments of non-native species is well known from ecological invasion studies (e.g., Banasaik & Meiners 2009; Cassey *et al.* 2008).

The second most important trait that determined the probability of successful establishment of tree species in the monodominant forests was wood density. Species with higher wood density had a greater probability of establishing in the monodominant forests. However, slow-growing, shade tolerant species with high wood density are very similar to *G. dewevrei* and probably occupy the similar niche as the monodominant species. But wood density being a significant determinant, alongside light requirement, suggests that high wood density may confer some other advantages. One possible benefit is that having heavy wood might reduce the probability of physical damage caused by falling debris under the closed *Gilbertiodendron* canopy. Wood density is strongly positively correlated to wood strength and stiffness (Chave *et al.* 2009a; van Gelder *et al.* 2006). Due to the denser canopy of *Gilbertiodendron*, the damage frequencies in monodominant forests may be higher as compared to mixed forests. The importance of denser and tougher wood in plants growing under closed canopy is supported by studies showing that the closed forests have higher damage rates than in more open areas (e.g., Gartner 1989); and wood density is positively related to the sapling

survival of forest tree species (Muller-Landau 2004). The reduction of species richness among stems with dbh >10 cm in the monodominant forests compared to species richness including individuals >1 cm dbh by Makana *et al.* (2004b) might be due to the high mortality among smaller trees (dbh <10 cm) caused by the falling debris of *Gilbertiodendron*. Lending credence to this speculation, studies have shown that although falling debris can cause high mortality in saplings (Clark & Clark 1992), physical damage has become less important once saplings have reach a dbh >10 cm (van de Meer & Bongers 1996). Therefore, having stronger wood may be an important factor that may confer an advantage for a species to grow beyond 10 cm in the monodominant forests.

The third most important trait for the species establishment in monodominant forests is their light requirement for seedling establishment. Pioneer species that demand full sunlight for seedling establishment (Kyereh *et al.* 1999) will be affected under *Gilbertiodendron* forest shade. This is because the monodominant forests have lower light penetration in the understorey than the mixed forest due to the relatively homogeneous, contiguous crowns of *G. dewevrei* (Makana *et al.* 2004; Torti *et al.* 2001). My study also shows that *Gilbertiodendron* forests had greater number of very large trees (dbh >60 cm) and these trees could cast deep shade. Moreover, pioneer species may fail to establish to maturity under the monodominant canopy because the falls of large *G. dewevrei* due to natural mortality are relatively uncommon in the monodominant forests. Thus, fewer large gaps are present to provide direct sunlight for the light demanding species to recruit to maturity (personal observations). All the common species with at least one individual per hectare sampling area in my monodominant forest plots were non-pioneers. The examples of these non-dominant species that can germinate under the forest shade were *Angylocalyx pynaerthii*, *Carapa procera*, *Desbordesia glaucescens*, *Staudtia stipitata*, *Pentaclethra macrophylla*, *Strombosia pustulata*, *Trichoscypha acuminata* and *Mammea africana*

My data set of species composition of the monodominant and mixed forests is a valuable resource for studying the factors underlying successful establishment of tree species in monodominant forests. However, the value of this data set may be compromised by the lack of

information of tree species with dbh <10 cm in the monodominant forests. Thus, only if I gather appropriate data of all seedlings and saplings, I do not know the true species richness in the monodominant forests. On the other hand, identifying species richness and the characteristics of the established non-dominant tree assembly may be more ecologically meaningful because the young saplings that fail to complete their life cycles might have limited contributions or influence on the functioning of the ecosystem.

As *G. dewevrei* is a valuable species for local timber industry, my findings may have important implications for the monodominant forest management. Exploiting *G. dewevrei* may substantially increase open areas and the colonization by species with low wood density (i.e., successional species). Hence, harvesting techniques and patterns that do not consider the ecological processes that underpin existing hardwood species distributions and abundances in the *Gilbertiodendron* forests will increase the risk of these species being replaced by those with lower-density wood. This will ultimately influence the availability of species with heavy wood, which is valuable for timber industry, in the monodominant forests.

3.5. Summary

- Based on taxon sampling curves, monodominant *Gilbertiodendron* forest had lower species richness, species density and population density than its adjacent mixed forest in terms of stem with dbh ≥ 10 cm.
- After controlling for phylogeny, the three most important determinants of the likelihood of successful establishment of non-dominant species in the *Gilbertiodendron* forests were: (1) relative abundance in adjacent mixed forest—the presence of a greater number of individuals in the mixed system significantly increased the establishment success of the tree species in the adjacent *Gilbertiodendron* forest; (2) wood density—species with relatively higher wood density had a greater chance of establishing in the monodominant forest; and (3) light requirement for seedling establishment—shade-tolerant species have a higher success rate to grow in the shady monodominant system.

- Over-harvesting of *Gilbertiodendron dewevrei* may substantially increase open areas and the colonization by less valuable timber species with low wood density (i.e., successional species).

4. Above-ground tree growth and fine litter productivity in relation to tree species diversity

4.1. Introduction

Plant biomass production (i.e., net primary production) provides the ‘fuel’ for heterotrophs to survive. Understanding the consequences of declining diversity on plant production is becoming increasingly important given the high rate of species loss in natural ecosystems due to human disturbance. It has been hypothesized that species diversity may influence net primary productivity in two ways: (a) areas with more species may have increased plant productivity caused by mechanisms such as resource-use complementarity and facilitation (see Chapter 1) or (b) production heavily depends upon the traits of individual species and their presence or absence (i.e., ‘sampling effects’; see Chapter 1).

A collection of studies have shown increasing plant productivity as the number of plant species increases (e.g., Naeem *et al.* 2000; Finke & Denno 2005). However, the most studied systems for this diversity-productivity effect are aquatic. These aquatic systems include freshwater pond mesocosms (Downing & Leibold 2002), salt marshes (Zedler *et al.* 2001), freshwater wetlands (Engelhardt & Ritchie 2002) and marine algae (Carpenter & Lodge 1986). These studies have reported a positive relationship between the diversity and biomass productivity, and the mechanism involved was mainly ‘sampling effects’. The applicability of the results from these studies to terrestrial systems is under debate (Hooper *et al.* 2005). This is because many of the observed conditions such as resource partitioning in terrestrial systems might not hold due to the higher connectivity in the aquatic systems (Giller *et al.* 2004).

In contrast to the aquatic ecosystems, the range of terrestrial systems being investigated is limited. Grassland has been the terrestrial system of choice used to test diversity-productivity hypothesis (e.g., Naeem *et al.* 2000; Loreau *et al.* 2002). These studies have reported that increasing species richness had a significant positive effect on the plant biomass production. The mechanisms explaining enhanced productivity with increasing plant species were sampling effects, species facilitation and resource-use complementarity, and these mechanisms were not

mutually exclusive (Hooper *et al.* 2005). However, we can not extrapolate our understanding from the grassland to other terrestrial systems because the ecosystem function responses may vary for different system types under different environmental conditions (Hooper *et al.* 2005). Therefore, we need to test the generality of the diversity-productivity relationship derived from these simplified systems using other more complex systems.

Observational comparisons across ecosystem types have suggested that the diversity-productivity relationship is not straightforward. Ecosystems in the tropics are generally productive and species rich, while those in the high latitude regions are the opposite (Waide *et al.* 1999). Furthermore, there are some relatively more productive ecosystems that harbour lower diversity. For example, coastal marsh communities that have low species richness (Bertness & Ellison 1987) are marked for their relatively high productivity (Waide *et al.* 1999). A tidal marsh in Louisiana that had plant species density of <11 species per m² was reported to have primary productivity up to 39 Mg dry mass ha⁻¹ yr⁻¹ (Gough *et al.* 1994). Another ecosystem that is characterized by its low species richness but high productivity is mangrove forest. However, its productivity is also determined by the abiotic factors such as tidal influences, runoff and water chemistry (Moore & Keddy 1989). Hence, caution is needed for the potential influences of extrinsic factors on diversity-productivity research. Within-site comparison might be a feasible approach to control for the influence of differing abiotic conditions and disturbance regime.

A within-site field study conducted by Hillbrand & Kahlert (2001) on algal productivity and herbivore composition has showed that diversity had stronger effects on productivity as compared to nutrient enrichment. Although neither diversity nor abiotic factor had any overriding effect of each other, this study showed a simultaneous top-down (i.e., abiotic effect) and bottom up (i.e., diversity effect) control of productivity.

'Natural' experiments have been conducted in Mediterranean forests (Vilà *et al.* 2007), temperate forests (Caspersen & Pacala 2001) and tropical tree plantations (Erskine *et al.* 2006), and have provided evidence of a positive association between species richness and wood production at the regional scale. However, no observational studies have been conducted in a

tropical forest yet. In this study, I explore if the positive diversity-functioning relationship remains valid within tropical rain forest communities characterized by differing levels of diversity. The use of a natural ecosystem experiment may result in confounding effects of abiotic conditions which are difficult to control. Nevertheless such study removes some consideration of initial conditions found in terrestrial experimental communities such as extinction order, species composition, relative species abundance and densities. This is because these parameters are determined by the system dynamics *per se*.

I hypothesized that a mixture of species that contains a higher species richness or diversity shows higher wood or litter- production in my study quadrats. Within my study quadrats, all species co-occurred on the same soil type, and were exposed to the same climatic conditions (see Chapter 2). The ecosystem function assessed in this paper is above-ground biomass (AGB) growth and fine litter productivity, the two major components of above-ground net primary productivity (ANPP).

4.2. Methods

4.2.1. Tree measurement

Three pairs of long-term forest monitoring 1 ha plots at the Dja Faunal Reserve were established in 2005 (for the description of the study area and plot establishment protocol, see Chapter 2). One plot of each pair contained a low-diversity of species dominated by *Gilbertiodendron dewevrei* while another plot, not more than 850 m away, contained a high diversity of species (for the species richness of the plots, see Table 4.1). Each 1 ha plot was subdivided into 25 quadrats (each 20 m × 20 m), in which each individual tree with dbh ≥ 10 cm or above buttresses was identified and measured. Tree measurement followed standard protocols (Phillips & Baker, 2002) to minimize the error introduced by inaccurate field measurement and variations between researchers.

Table 4.1 Number of stems with diameter at breast height (dbh) ≥ 10 cm and diversity index of the three pairs of 1 ha plots at the Dja Faunal Reserve. The pairs were G1-M1, G2-M2, and G3-M3. Dominance refers to the dominance of *Gilbertiodendron dewevrei* in terms of above-ground biomass (AGB) at 2005. AGB was estimated using the predictive regression model developed for moist forest stands involving tree height, diameter at breast height and wood mass density. Basal area was measured in 2005. ABG growth is the sum of all biomass increments plus newly recruited stems observed between 2005 and 2008. Litterfall productivity was measured between 2007 and 2008.

Forest type	Plot	Number of stems	Number of species	Fisher's alpha	Dominance (%)	Basal area (m ² ha ⁻¹)	Basal area growth (m ² ha ⁻¹ yr ⁻¹)	AGB (Mg dry mass ha ⁻¹)	AGB growth (Mg dry mass ha ⁻¹ yr ⁻¹)	Litterfall productivity (Mg dry mass ha ⁻¹ yr ⁻¹)
Monodominant	G1	307	33	9.37	73	33.45	0.43	560.65	8.11	12.84
	G2	347	35	9.71	85	30.74	0.33	554.57	5.99	17.73
	G3	372	39	10.98	97	31.87	0.23	543.19	4.26	13.04
Mixed	M1	430	107	45.65		23.71	0.41	298.33	4.93	16.45
	M2	473	130	59.19		26.38	0.31	333.78	4.02	19.77
	M3	407	104	45.13		23.19	0.38	246.96	4.51	17.10

The points of measurement for the trees were at 1.3 m where possible, and were painted for future reference. When buttress roots or bole irregularities occurred at 1.3 m, the points of measurement were then taken at 0.5 m above the highest points of buttress roots or at 2 cm below the lowest point of bole irregularities. An optical method using digital camera was used for 20 cases where the height of their buttress roots was >5 m. In early March of 2006, 2007 and 2008, I remeasured the dbh of all surviving trees ≥ 10 cm in all plots using the standard measurement protocol. I also incorporated new trees of dbh ≥ 10 cm recruiting into each plot.

For the 20 trees whose initial dbh was estimated using the optical method, I estimated the growth rates using median growth rate of the sized class ≥ 40 cm (i.e., 60 dbh values from all censuses) (Phillips & Baker 2002). From all censuses, I screened the dbh census data for obvious typographical errors (7 dbh values), accidental missing data (14 dbh values) and for growth rate less than -0.3 cm yr^{-1} or more than 2 cm yr^{-1} (66 dbh values). Missing data was replaced by values estimated by interpolation or extrapolation from other censuses. For the growth rates that were outside the reasonable range, I checked them in the field. However, final decisions on any corrections were made on a tree-by-tree basis. For example, growth rate $>2 \text{ cm yr}^{-1}$ for pioneer species is legitimate. Only 1.6 % of the dbh census data was corrected (i.e., 147 dbh values from all censuses). In other words, there were 6 dbh values corrected census⁻¹ plot⁻¹.

4.2.2. Estimations of AGB growth

AGB growth is the increment of AGB, plus the AGB of newly recruited trees, expressed as an annual rate (Lewis 2004a). AGB of a tree was estimated using the predictive regression model developed for moist forest stands involving H , ρ and D (Chave *et al.* 2005):

$$\text{AGB} = \sum \exp((-2.977 + \ln(\rho D^2 H)) \equiv 0.0509 \times \rho D^2 H \quad (1)$$

where ρ is wood mass density, D is dbh and H is tree height. I obtained wood mass density (see Chapter 3 for definition) for each species that occurred in my plots from Lewis *et al.* (2009), which compiled the data from 34 sources (e.g., Bolza & Keating 1972; Rijdsdijk & Laming 1994). I took mean genus-level wood density for individual stems with no species-specific data

(see Chapter 3). I used mean wood density of all stems within a plot for stems with genus-level and family-level data not available.

Another important variable in the estimation of AGB is the tree height, H (Chave *et al.* 2005). Total height of at least 10 trees from each dbh (D) size class of 10–20 cm, 20.1–30 cm, 30.1–40 cm, 40.1–50 cm and all trees >50 cm in each plot, excluding broken trees, was measured with a clinometer. To estimate H of each individual tree ≥ 10 cm, I fitted the non-linear, three-parameter Weibull equation (equation 2) for each plot based on relatively large sample sizes of direct total height measurement (Fang & Bailey 1998; Lewis *et al.* 2009).

$$\log H = a*(1 - \exp(b*(\log D^c))) \quad (2)$$

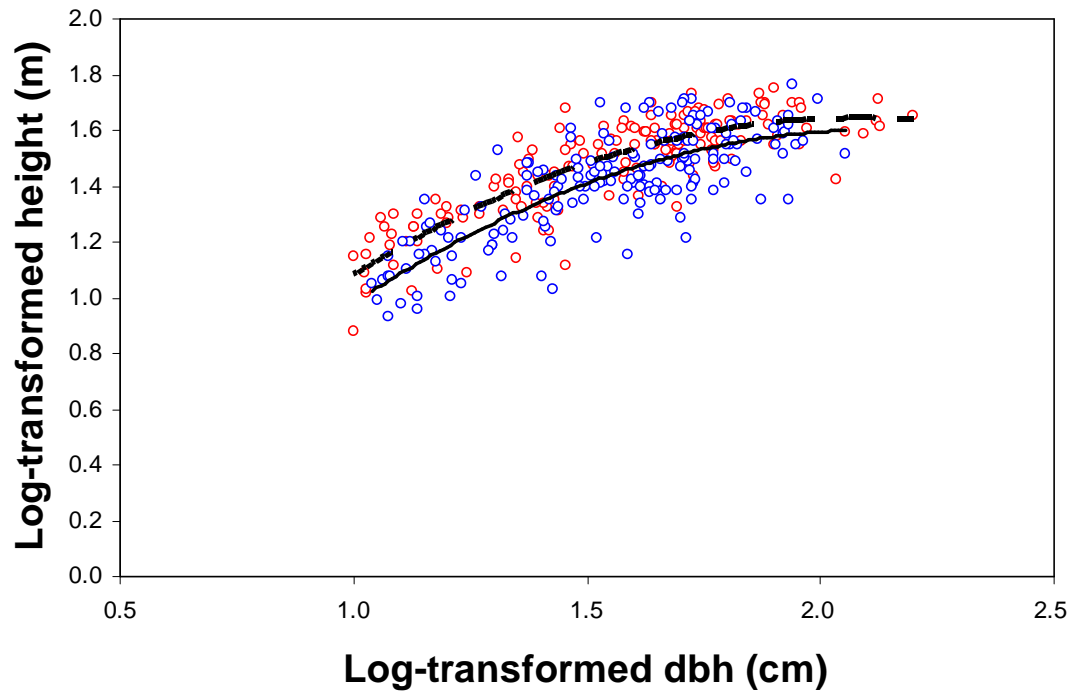
Plots within the same forest type had the standard errors (SE) of the constants in their equations overlapped. Therefore, these plots had statistically indistinguishable equations. This suggests that the plots within each forest type were not significantly different in terms of H/D allometry. The following equations relate log-transformed D (cm) to log-transformed H (m) in the monodominant forests (equation 3; $r^2 = 0.75$, $n = 173$) and mixed forest (equation 4; $r^2 = 0.65$, $n = 183$), respectively, when I pooled the data of each forest type:

$$\log H = 1.705*(1 - \exp(-0.991*(\log D^{1.763}))) \quad (3)$$

$$\log H = 1.681*(1 - \exp(-0.871*(\log D^{1.829}))) \quad (4)$$

However, I did not pool all data from the two forest types to construct a general equation because the two forest types had significantly different equations. The general linear model (GLM) analyses of covariance (with forest type as a fixed factor) shows that the forest type ($F = 25.08$, $P < 0.001$) had a highly significant effect on the relationship between D and H (Fig. 4.1). Therefore, I used separate equation for each forest type to estimate the height of trees that were not measured, for inclusion in allometric equations (equation 1) to calculate biomass.

Figure 4.1. Non-linear, three-parameter regressions of tree height on tree diameter at breast height (dbh) for monodominant forest (red circles; dotted line) and mixed forest (blue circles; solid line).



I used actual heights (instead of H) if available and calculated the AGB of each quadrat for 2005, 2006, 2007 and 2008, whereby AGB is the sum of all AGB of all trees in a quadrat. I calculated the stand-level AGB growth (expressed as an annual rate), as a measure of wood production, by summing the increments of AGB of surviving trees and AGB of new trees that recruited into a plot between 2 consecutive census (following Lewis *et al.* 2004a; Chave *et al.* 2008). Also, I calculated the AGB net change (expressed as an annual rate) by summing the AGB increments and AGB of newly recruited trees into a plot, and subtracting the AGB of the dead trees (mortality losses) between the census intervals (Lewis *et al.* 2004a).

It has been claimed that it may sometimes be better to exclude tree height in biomass estimations (Williams & Schreuder 2000). To assess if the calculations of AGB were sensitive to the estimations of H , I recalculated AGB of each plot using predictive regression model involving only ρ and D (Chave *et al.* 2005):

$$\text{AGB} = \rho * \exp(-1.499 + 2.148\ln(D) + 0.207((\ln(D))^2 - 0.0281 (\ln(D))^3) \quad (5)$$

Besides AGB derived from the two estimation procedures, I also calculated the total basal area of the two forest types, and their basal area growth and net change (expressed as an annual rate).

4.2.3. Estimations of fine litter productivity and ANPP

In late March 2007, I placed three standing litterfall traps (0.5 m × 0.5 m, 1 mm mesh; 1 m above the ground) and three ground traps (0.5 m × 0.5 m, no mesh; on the ground) in each of 10 randomly selected quadrats in each of six plots. All traps were randomly placed at least 5 m away within the perimeter of the quadrats to minimize the influence of the adjacent quadrats (i.e., edge effect) (Wardle & Zackrisson 2005). For a period of one year (April 2007–March 2008), I fortnightly collected the leaves, woody litter (wood diameter <1 cm), flowers, fruits and seeds from the standing traps; and fine wood debris (wood diameter ≥1 cm to 10 cm) from the ground traps. The total amount of fine litterfall (expressed in Mg dry mass ha⁻¹), derived from each of 10 quadrats in each of six plots was used (1) to determine if there was a difference in

fine litterfall productivity between the two forest types and (2) to determine if the fine litterfall mass correlates with species diversity at a small-scale level within each forest type.

Since the total area of the standing traps covered only a small proportion of a quadrat (approximately 0.2%), I predicted that species richness and diversity index at quadrat level might not truly reflect the plant diversity that contributes to the litterfall mass. Thus, I developed a measure of species richness (hereafter trap species number) to describe the α -diversity contributing to the litterfall mass, calculated in two steps. First, I estimated the number of vascular plant species based on the wet leaves collected fortnightly from the three standing traps in a quadrat, with unidentified leaves identified to morphospecies. Therefore, the total number of vascular plant species for every collection was counted for each quadrat containing traps. Second, I calculated the mean, median and modal plant species number from all collections for each quadrat. In using the mean, I assume that the standing traps captured only litter of species in its immediate surrounding, while calculating the median and modal species number dampens any accidental contribution of new species further from the quadrats.

I calculated the above-ground net primary productivity (ANPP) for each of quadrats with litterfall traps by summing the mean AGB growth derived from the 2005 to 2008 census interval and the total litterfall productivity from April 2007 to March 2008 (expressed in Mg dry mass ha⁻¹). Again, I determined whether there is a difference in ANPP between the two forest types and whether ANPP correlates with species diversity and richness (derived from late March 2007 census) at a small-scale level within each forest type.

4.2.4. Statistical analyses

To determine the effects of the number of species on AGB growth, for each quadrat I counted the number of tree species identified. Besides quadrat species number (number of species per quadrat), I used a diversity index, which takes the community composition such as the relative abundance of different species into account, to test the diversity effect. I calculated the Simpson's diversity index for each quadrat: $1/\sum p_i^2$ where abundance is based on total number

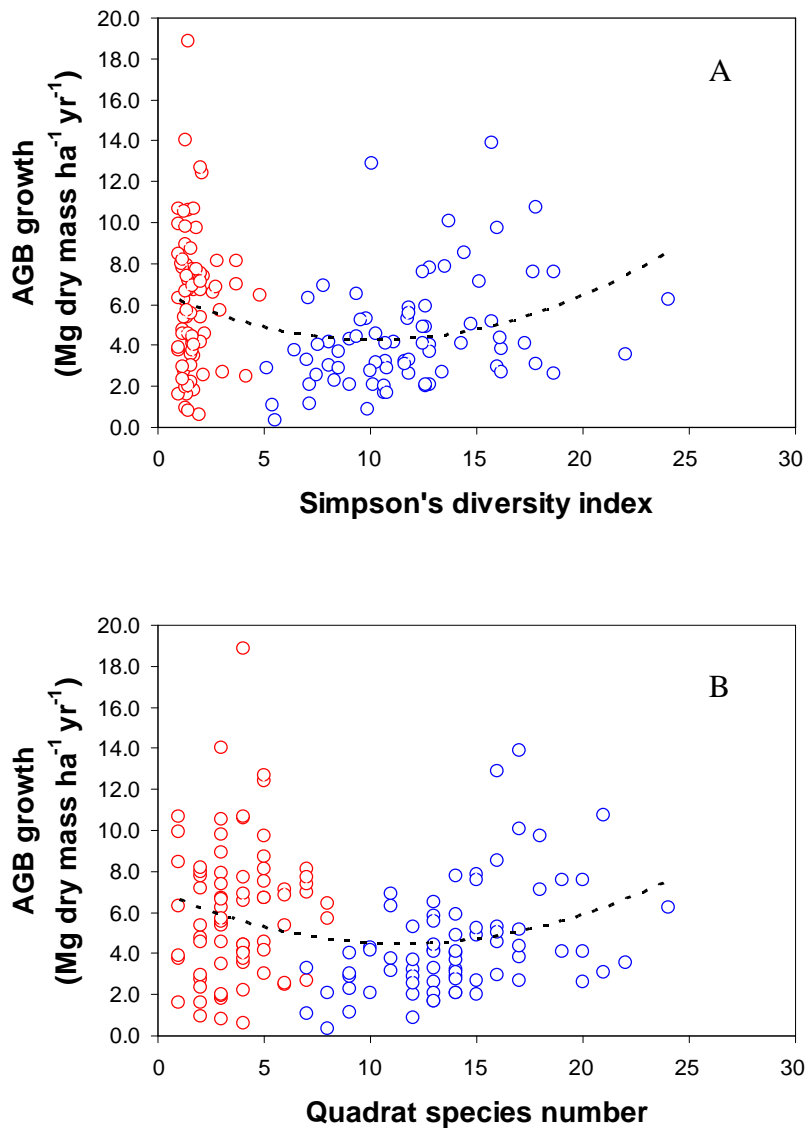
of individuals and where p is the proportion of total number of species for an individual species (i). I chose Simpson's diversity index because it is straightforward to interpret. For example, when the dominant species, *G. dewevrei*, exists on its own in a quadrat, the Simpson's index value is one. The index value is two if two species exist with an equal number of individuals, and so forth. Simpson's index value is always lower than the total number of species because multiple species can co-exist at unequal proportion of individuals. Besides calculating Simpson's diversity index at quadrat level, I counted the number of stems and calculated the Fisher's α value (a measurement of tree species diversity) for each 1 ha plot using: $S = \alpha \times \ln(1 + n/\alpha)$ where S is the number of species and n is the number of individuals.

Another component of diversity, species evenness which measures how well distributed abundance is among species within a community, has been found to be influential on some plant diversity-productivity studies (e.g., Wilsey & Potvin 2000). I measured species evenness (E) for each quadrat by expressing Simpson's index as a proportion of total number of species: $E = \text{Simpson's index} / \text{total species number}$.

To determine if monodominant forests are different from mixed forests, I compared the stand-level basal areas and AGB (measured in 2005), AGB growth (derived from 2005–2008), AGB net change, litterfall productivity (derived from April 2007–March 2008) and ANPP between the two forest types ($n = 3$ pairs).

For exploratory analyses, I pooled data of all quadrats from monodominant forests and mixed forests to quantify the overall relationship between diversity (quadrat species number and Simpson's diversity index) and the stand-level productivity (AGB growth, $n = 150$). The scatterplots of pooled data show (1) both species richness and diversity index of the two forest types had bimodal distributions, and (2) when fitted with a quadratic regression model ($P < 0.05$), the two forest types had different trends in the diversity-productivity relationship (Fig. 4.2). Thus, the data were analysed separately for each forest type.

Figure 4.2 Scatterplots of above-ground biomass (AGB) growth from 2005 to 2008 along gradients of Simpson's diversity index (A) and species number (B) using pooled data from monodominant and mixed forests. Each circle represents a quadrat. Red circles represent monodominant forest quadrats ($n = 150$) and blue circles represent mixed forest quadrat ($n = 150$). The dotted lines show the significant quadratic regressions ($P < 0.05$) when fitted with the pooled data.



For each forest type, I plotted AGB growth as a function of quadrat species number, Simpson's diversity index and quadrat species evenness. In addition, I plotted litterfall productivity and ANPP as a function of quadrat species number, Simpson's diversity index, mean trap species number, median trap species number and modal trap species number. I checked and then transformed the data to ensure normality before using a parametric Pearson correlation test. Otherwise, I used non-parametric Spearman's rank test for data that were non-normally distributed even after transformation. Only diversity measures that have significant correlations were further investigated to control for potentially confounding effects on productivity. Generally, productivity increases with stand-level biomass and stem density (Keeling & Phillips 2008). Also, forest productivity of a study location can be affected by the local environmental conditions (e.g., climate and soil properties; Hector *et al.* 1999). To test the effects attributable to diversity (i.e., species number, Simpson's index or trap species number) and to test for the dependence of residual variation on size-dependent shifts in growth, stem density and spatial variation in abiotic condition, I used general linear model (GLM) analyses of covariance with type III sums of squares. This is the most conservative test that determined if each variable investigated (diversity, in terms of quadrat species number, Simpson's index or trap species number; stem density; stand-level biomass; and plot location) could explain a significant portion of residual variance after the other variables had already been accounted for.

Lastly, to determine if the AGB growth of the dominant *G. dewevrei* was faster than other relatively abundant species in the reserve, I compared, using GLMs, the AGB growth of *G. dewevrei* along the gradient of tree size in dbh with each of species that had more than 20 individuals within the 6 ha.

4.3. Results

4.3.1. Basal area

In all six plots, I identified 2336 individual stems representing 194 species and 17 morphotypes (Table 4.1; also see Chapter 3). The monodominant forests had a significantly higher basal area

($\pm 95\%$ confidence interval; $n = 3$) in 2005 of $32.02 \pm 1.54 \text{ m}^2 \text{ ha}^{-1}$ as compared with that of the mixed forests of $24.43 \pm 1.93 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 4.3). The mean difference in basal area between the two forest types was $7.59 \pm 3.22 \text{ m}^2 \text{ ha}^{-1}$.

The basal area growth ($\pm 95\%$ confidence interval; $n = 3$) in the monodominant and mixed forests are not significantly different, being observed at $0.33 \pm 0.11 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ and $0.37 \pm 0.06 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$, respectively (Wilcoxon signed ranks test, $n = 3$, $P = 1.00$). The mean of paired differences between the two forest types was $0.04 \pm 0.10 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$. The basal area growth was not different among all six plots, except that one monodominant forest plot (G1) had significantly greater growth than another (G3) (Fig. 4.4A). The comparison of 18 estimates of basal area growth across three census intervals did not show any patterns between the two forest types (Fig. 4.4B; Friedman test, $P = 0.56$). The scatter-plot of basal area growth along the Fisher's α of all plots ($n = 6$) did not show significant relationship (Fig. 4.4C).

The basal area net change between 2005 and 2008 observed in the monodominant forests and mixed forests were $0.13 \pm 0.18 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ and $-0.03 \pm 0.38 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, respectively (Fig. 4.5A). All sets of 95% confidence intervals overlapped among all of six plots indicating that there was no significant difference in their mean basal area net change (Fig. 4.5A). The basal area net change between the two forest types did not significantly differ (Wilcoxon signed ranks test, $n = 3$, $P = 0.59$). The comparison of 18 estimates of basal area net change among the six plots across three census intervals did not show any patterns between the two forest types (Fig. 4.5B; Friedman test, $P = 0.56$). The scatter-plot of mean annual basal area net change along the Fisher's α of all plots ($n = 6$) did not show significant relationship between annual basal area net change and diversity index (Fig. 4.5C).

Figure 4.3 Estimations of basal area in 2005 for all six 1 ha plots at the Dja Faunal Reserve. G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.

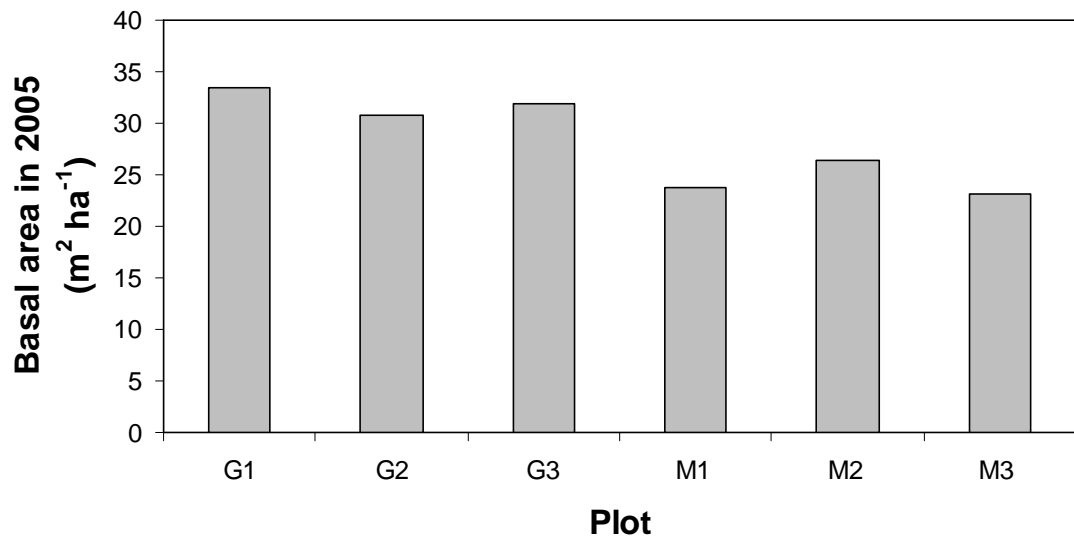


Figure 4.4 Annualized three years basal area growth between 2005 and 2008 for all six plots at the Dja Faunal Reserve (A); comparisons of 18 estimates of basal area growth from the three census intervals and six plots (B); and scatter-plot of basal area growth along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles) (C). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.

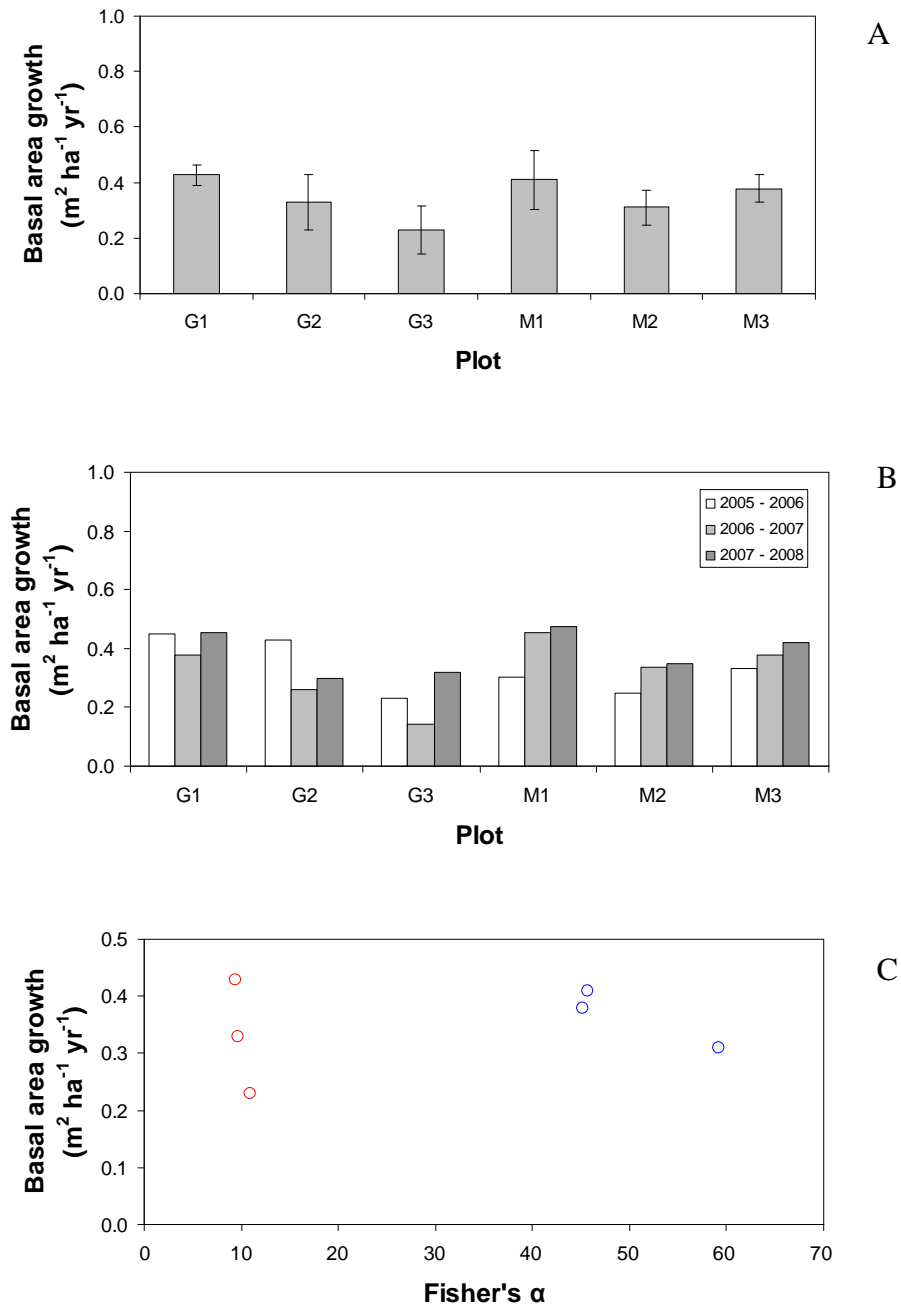
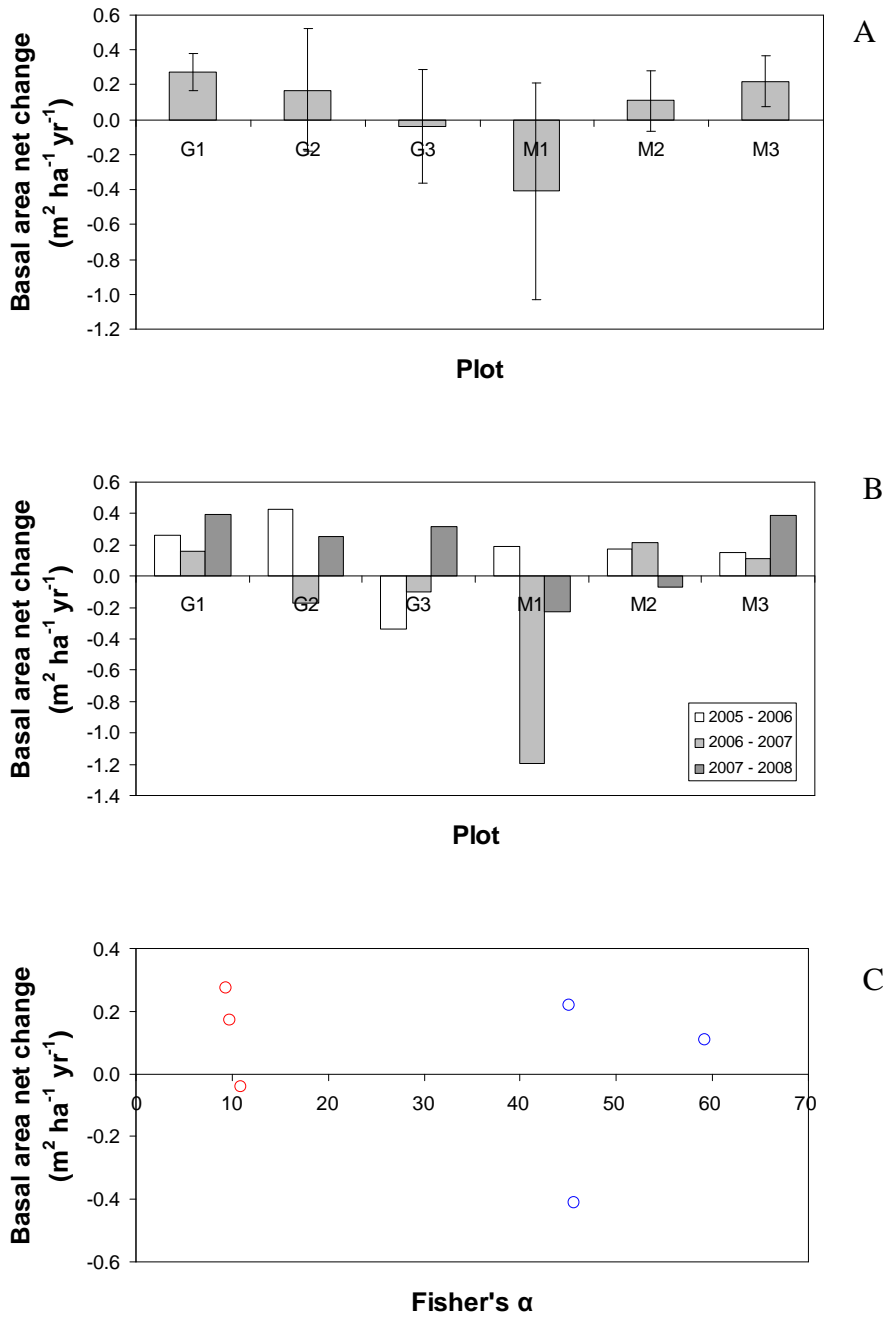


Figure 4.5 Annualized three years basal area net change between 2005 and 2008 for all six plots at the Dja Faunal Reserve (A); comparisons of 18 estimates of basal area net change from the three census intervals and six plots (B); and scatter-plot of mean basal area net change along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles) (C). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.



4.3.2. Above-ground biomass

Based on the biomass-diameter-height regression model (equation 3), the monodominant forests had a significantly higher AGB (\pm 95% confidence interval; $n = 3$) of 552.80 ± 10.03 Mg dry mass ha^{-1} as compared with that of the mixed forests of 293.02 ± 49.40 Mg dry mass ha^{-1} in 2005. The mean of paired differences between the two forest types was 259.78 ± 42.76 Mg dry mass ha^{-1} . For comparison purposes, I calculated the AGB of the monodominant and mixed forests using the biomass-diameter regression model (equation 4), and they yielded 537.35 ± 14.56 Mg dry mass ha^{-1} and 314.27 ± 46.70 Mg dry mass ha^{-1} , respectively (Fig. 4.6, A & B). There was no significant difference in the AGB between the two biomass estimation procedures. Hence, all AGB mentioned hereafter refer to the values derived from the biomass-diameter-height regression model.

The mean AGB growth (\pm 95% confidence interval; $n = 3$) between 2005 and 2008 for the monodominant forests was 6.12 ± 1.63 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$ and was not significantly higher than 4.49 ± 0.54 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$ of the mixed forests (Wilcoxon signed ranks test, $n = 3$, $P = 0.29$). The mean of paired differences between the two forest types was 1.64 ± 1.97 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$. All plots had their sets of 95% confidence intervals overlapped except for two of the monodominant forest plots (G1 & G3; Fig. 4.7A). Out of nine monodominant-mixed forest pairs of estimates across three census intervals, eight pairs had the monodominant forest plots with a greater AGB growth than their counterparts (Fig. 4.7B). However, the AGB growth of the two forest types were not statistically different (Friedman test, $P = 0.08$). The scatter-plot of mean AGB growth along the gradient of Fisher's α ($n = 6$) did not reveal any relationship between AGB growth and Fisher's α diversity index.

Figure 4.6 Estimations of above-ground biomass in 2005, based on biomass-diameter-height regression model (A) and biomass-diameter regression model (B) for all six 1 ha plots at the Dja Faunal Reserve. G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.

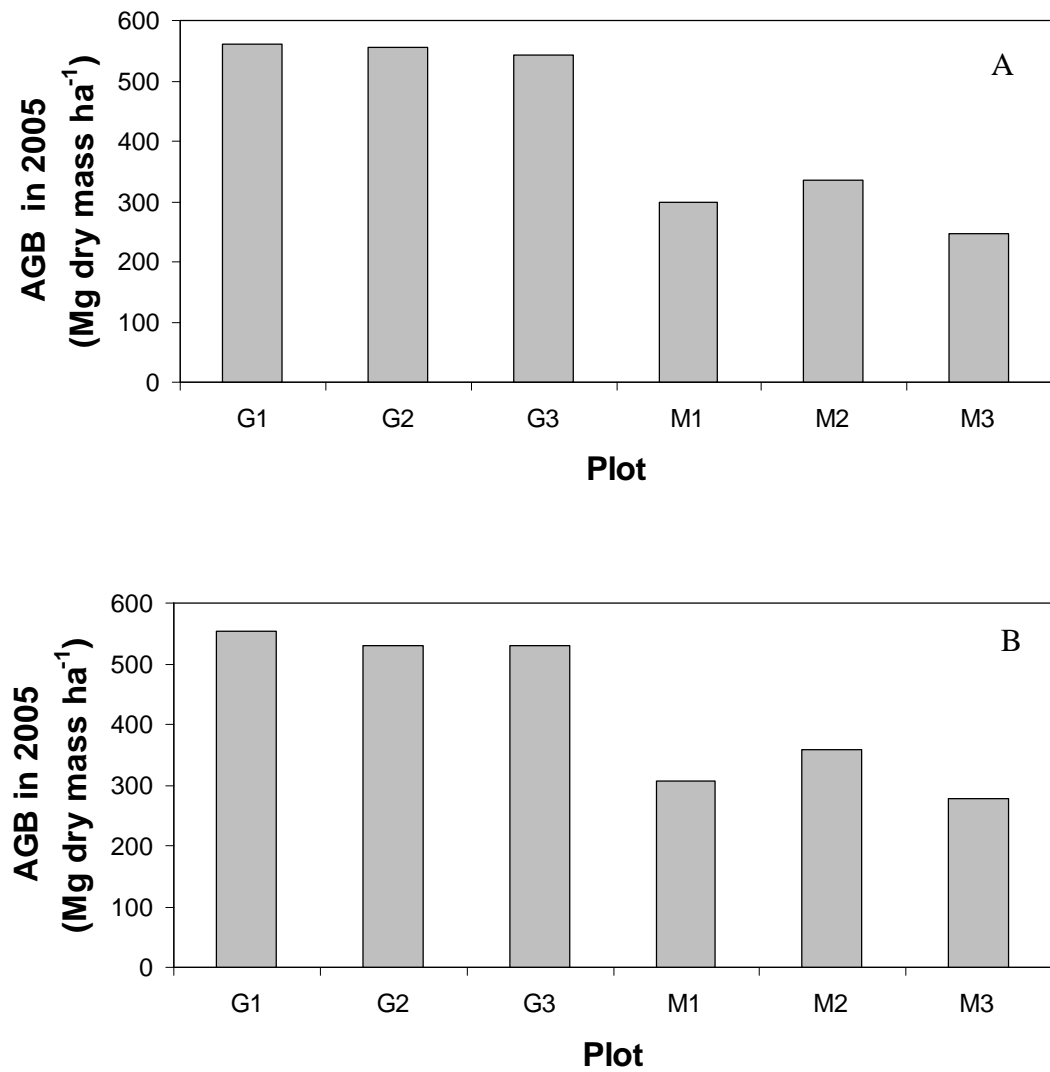
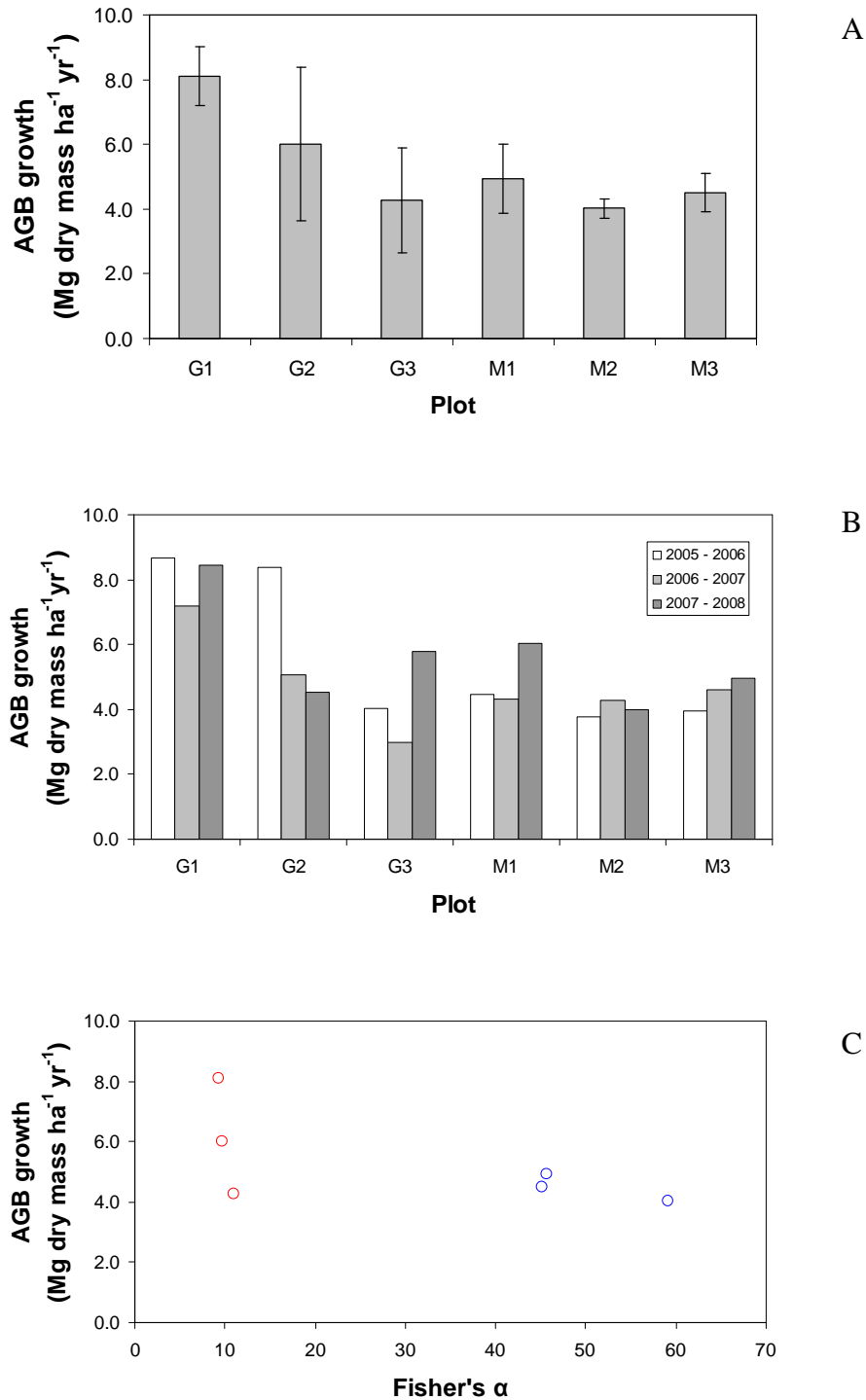


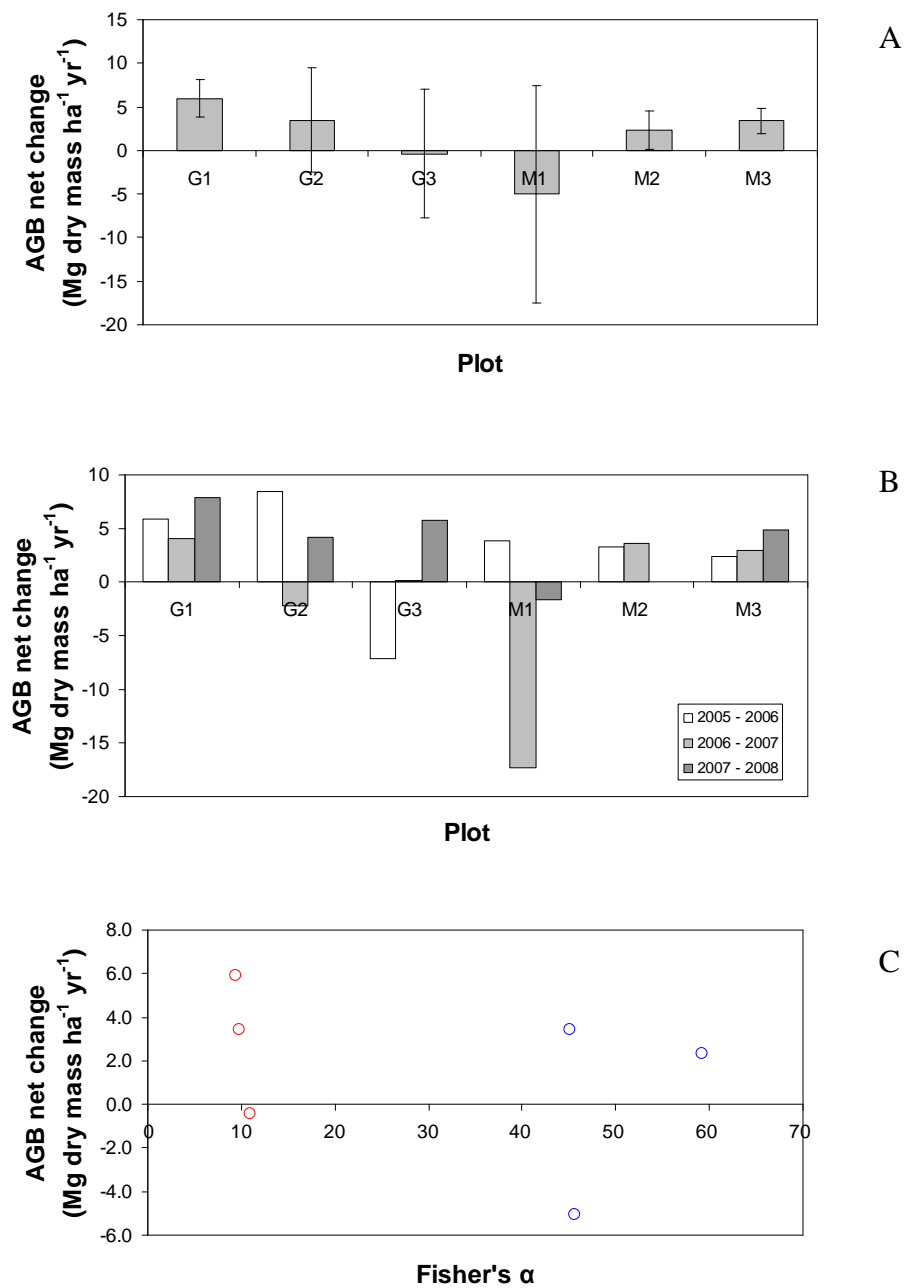
Figure 4.7 Annualized three years above-ground biomass (AGB) growth between 2005 and 2008 for all six plots at the Dja Faunal Reserve (A); comparisons of 18 estimates of AGB growth from the three census intervals and six plots (B); and scatter-plot of mean AGB growth along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles) (C). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.



The problematic diameter census data and the use of digital camera to measure 20 trees with high buttresses potentially introduce uncertainty into estimates of AGB growth. Optical method is certainly less precise than a tape-measure because it cannot take the irregularities in bole shapes into account and is a potential source of error. To test if the estimated growth of the 20 trees with high buttress affected my results, I made an assumption that these trees had no AGB growth and recalculated the AGB growth for both forest types. Based on this assumption, the AGB growth (\pm 95% confidence interval; $n = 3$) for the monodominant and mixed forests are 5.83 ± 1.04 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$ and 4.32 ± 0.55 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$, respectively; both decreased by approximately 0.2 Mg dry mass $\text{ha}^{-1} \text{year}^{-1}$. These estimates reconfirmed that the AGB growth between the two forest types did not significantly differ.

Between 2005 and 2008, the mean AGB net change (\pm 95% confidence interval; $n = 3$) of 2.98 ± 3.63 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$ and 0.23 ± 5.21 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$ were observed for the monodominant and mixed forests, respectively. The mean AGB net change was not significantly different between the two forest types (Wilcoxon signed ranks test, $n = 3$, $P = 0.59$) and among all the six plots (Fig. 4.8A). The AGB net change values for all six plots across the three census intervals did not show any distinct pattern between the two forest types (Fig. 4.8B; Friedman test, $P = 0.56$). Likewise, there is no significant relationship between annual AGB net change and Fisher's α values of the plots ($n = 6$; Fig. 4.8C).

Figure 4.8 Annualized three years above-ground biomass (AGB) net change between 2005 and 2008 for all six plots at the Dja Faunal Reserve (A); comparisons of 18 estimates of AGB net change from the three census intervals and six plots (B); and scatter-plot of mean AGB net change along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles) (C). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.



4.3.3. Diversity and above-ground biomass growth

In the monodominant forests, AGB growth did not significantly correlate with all diversity variables (i.e., quadrat species number, Simpson's diversity index and species evenness) (Fig. 4.9, A–C). In the mixed forest, however, AGB growth significantly correlated with the quadrat species number (Pearson coefficient = 0.482, $P < 0.001$; Fig. 4.10A) and Simpson's diversity index (Pearson coefficient = 0.399, $P < 0.001$; Fig 4.10B). The relationships have the best curve estimation regression statistics for a quadratic regression model and remain highly significant (quadrat species number: $r^2 = 0.27$, $P < 0.001$; Simpson's diversity index: $r^2 = 0.22$, $P < 0.001$; Table 4.2). But species evenness had no significant correlation with AGB growth in the mixed forest (Fig. 4.10C).

GLM analyses of covariance were performed for the mixed forest only. The results show that quadrat species number ($F = 6.69$, $P < 0.05$), stand-level AGB in 2005 ($F = 19.84$, $P < 0.001$) and plot location ($F = 3.34$, $P < 0.05$) significantly impacted the stand-level AGB growth—in models with log-transformed AGB growth as the dependent variables; quadrat species number, stem density and log-transformed AGB as covariates; and plot location as random factor. More importantly, the effect of species richness remained significant when the effects of stand-level AGB, stem density and plot location were accounted for (Table 4.2).

Likewise, Simpson's diversity index ($F = 7.44$, $P < 0.01$) remained significant after stand-level AGB in 2005 ($F = 20.06$, $P < 0.001$), plot location ($F = 3.64$, $P < 0.05$), and stem density had been considered (Table 4.2). Our results suggest that between the quadrats with the same species richness or diversity index, there is a variation in their performance according to their original AGB.

Figure 4.9 Scatter-plots of above-ground biomass (AGB) growth along a gradient of species number (A) in monodominant forest; Simpson's diversity index (B); and species evenness (C). Each dot represents a quadrat ($n = 75$). No significant relationship was observed between AGB growth and diversity in the monodominant forest.

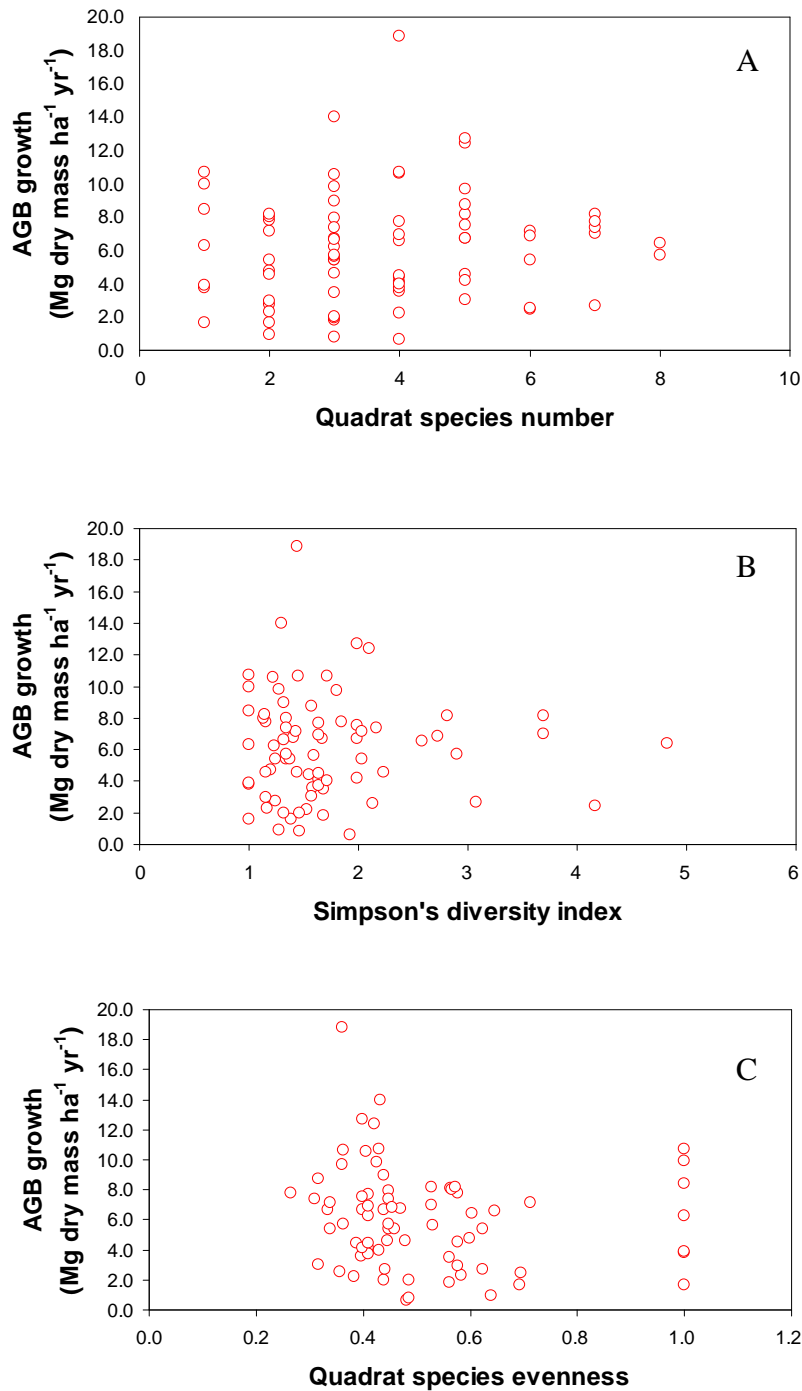


Figure 4.10 Scatter-plots of above-ground biomass (AGB) growth along a gradient of species number in mixed forest (A); Simpson's diversity index (B); and species evenness (C). Each dot represents a quadrat ($n = 75$). No significant relationship was observed between AGB growth and evenness.

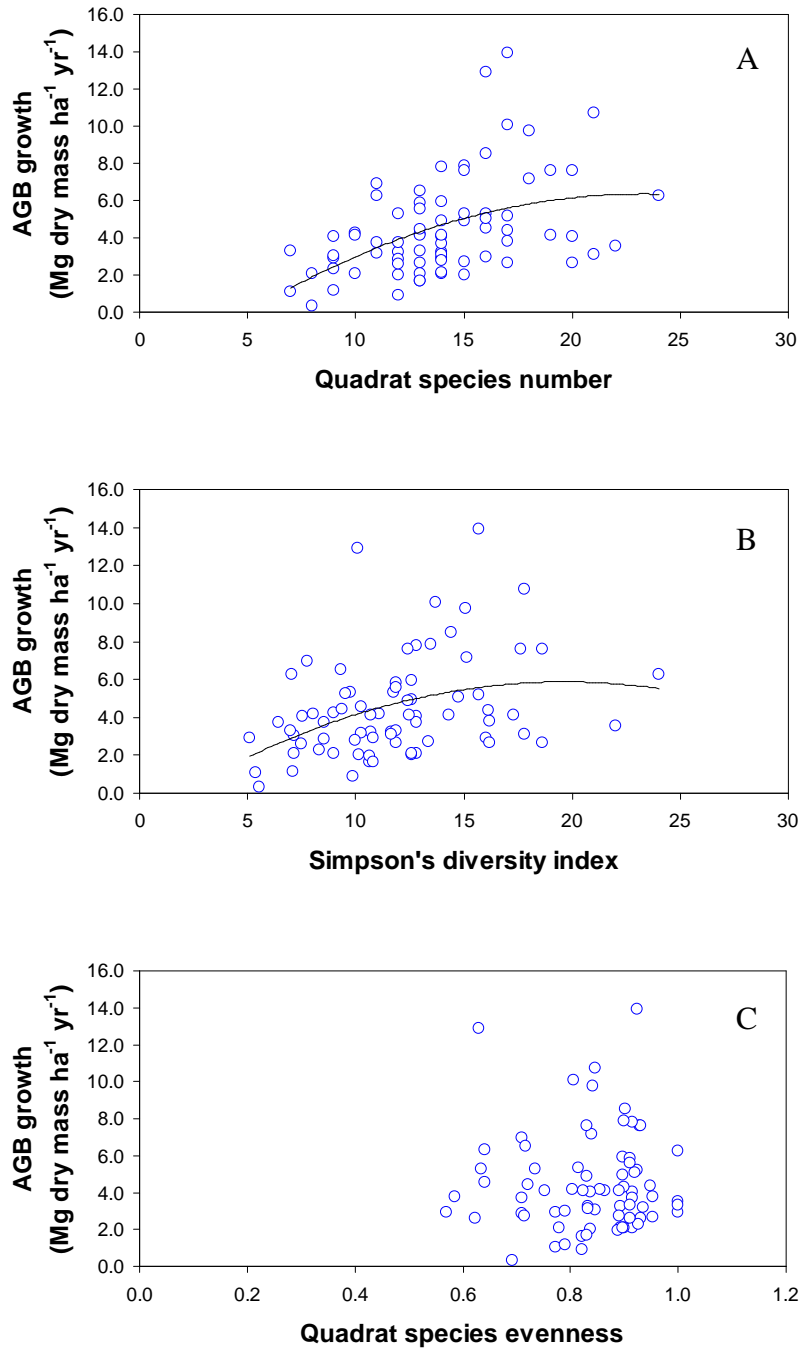


Table 4.2 Quadratic regressions and general linear model (GLM) analyses of covariance were performed on data from the mixed forest plots only. Statistics for diversity effects (quadrat species richness, Simpson's diversity index, or trap species number) in mixed forest on above-ground biomass (AGB) growth, litterfall productivity and above-ground net primary productivity (ANPP). Original AGB was the stand-level AGB measured in 2005 for the analyses of AGB growth ($n = 75$) and that was remeasured in 2007 for the analyses of litter productivity ($n = 30$) and ANPP ($n = 30$). All parameters were checked and then log-transformed, if necessary, to improve normality before analyses. $P < 0.01$ is denoted by ** and $P < 0.05$ is *.

	r^2	GLM analyses of covariance		
		F	P	
AGB growth				
Quadrat species number	0.27**	6.69	<0.05	*
Log-transformed original AGB (2005)		19.84	<0.01	**
Stem density (2005)		0.34	0.57	
Plot location		3.34	<0.05	*
Log-transformed Simpson's diversity index	0.22**	7.44	<0.01	**
Original AGB (2005)		20.06	<0.01	**
Stem density (2005)		0.25	0.62	
Plot location		3.64	<0.05	*
Litterfall productivity				
Mean trap species number	0.22**	9.80	<0.01	**
Log-transformed original AGB (2007)		8.13	<0.01	**
Stem density (2007)		2.32	0.14	
Plot location		1.12	0.34	
Median trap species number	0.21**	6.01	<0.05	*
Log-transformed original AGB (2007)		6.31	<0.05	*
Stem density (2007)		1.47	0.24	
Plot location		0.26	0.78	
ANPP				
Mean trap species number	0.13*	4.57	0.04	*
Log-transformed original AGB (2007)		10.37	<0.01	**
Stem density (2007)		1.30	0.27	
Plot location		0.22	0.80	

4.3.4. Litterfall productivity and ANPP

The litterfall productivity (\pm 95% confidence interval; $n = 3$) in the monodominant forest between April 2007 and March 2008 was 14.54 ± 3.13 Mg dry mass ha^{-1} and it was not significantly different from 17.77 ± 1.99 Mg dry mass ha^{-1} in the mixed forest (Fig. 4.11A). The mean of paired differences in litterfall mass between the monodominant and mixed forests was 3.23 ± 1.27 Mg dry mass ha^{-1} . Pair-wise comparison of the two forest types did not show any significant difference in the litterfall mass between the forest types (Wilcoxon signed ranks test, $n = 3$, $P = 0.109$). The scatter-plot of litterfall productivity along the Fisher's α of all plots ($n = 6$) did not show significant relationship between litterfall productivity and diversity index (Fig. 4.11B).

The litterfall productivity of the monodominant forests had no significant relationship with quadrat species number in 2007 (Fig. 4.12A) and Simpson's diversity index in 2007 as predicted (Fig. 4.12B). Yet mean trap species number (Fig. 4.13A), median trap species number (Fig. 4.13B) and modal trap species number also showed no significant relationship, which was not predicted (Fig. 4.13C).

Litterfall productivity between March 2007 and April 2008 in the mixed forest did not significantly correlate with quadrat species number at 2007 (Fig. 4.14A) and Simpson's diversity index at 2007 (Fig. 4.14B) that measure species richness and diversity at the quadrat level. However, litterfall productivity was significantly correlated with mean trap species number (Pearson coefficient = 0.46, $P < 0.05$; Fig 4.15A), and with median trap species number (Pearson coefficient = 0.42, $P < 0.05$; Fig. 4.15B). Their relationship remains significant ($r^2 \geq 0.21$, $P < 0.01$) in GLMs. The effect of mean trap species number remains highly significant ($F = 9.80$, $P < 0.05$) after stand-level biomass in 2007 ($F = 8.13$, $P < 0.01$; Table 2), stem density in 2007 and plot location were accounted for. Also the effect of median trap species number remains highly significant ($F = 6.01$, $P < 0.05$) after accounting for stand-level biomass in 2007 ($F = 6.31$, $P < 0.05$), stem density at 2007 and plot location ($P > 0.05$; no significant plot effect).

Figure 4.11 Mean litterfall productivity (n = 10 quadrats) between April 2007 and March 2008 for all six plots at the Dja Faunal Reserve (A); and scatter-plot of litterfall productivity along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.

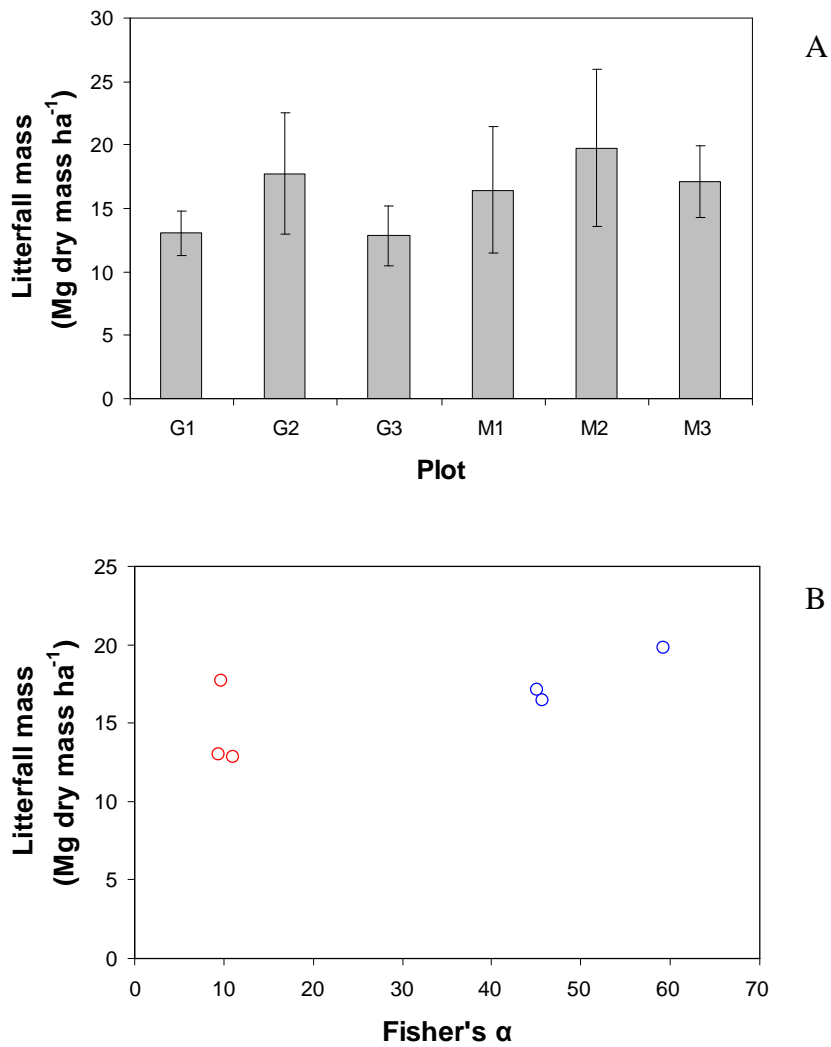


Figure 4.12 Scatter-plots of litterfall mass along a gradient of quadrat species number (A) and Simpson's diversity index (B) in monodominant forest. Each circle represents a quadrat ($n = 30$). No significant relationship was observed between litterfall mass and diversity variables at quadrat level.

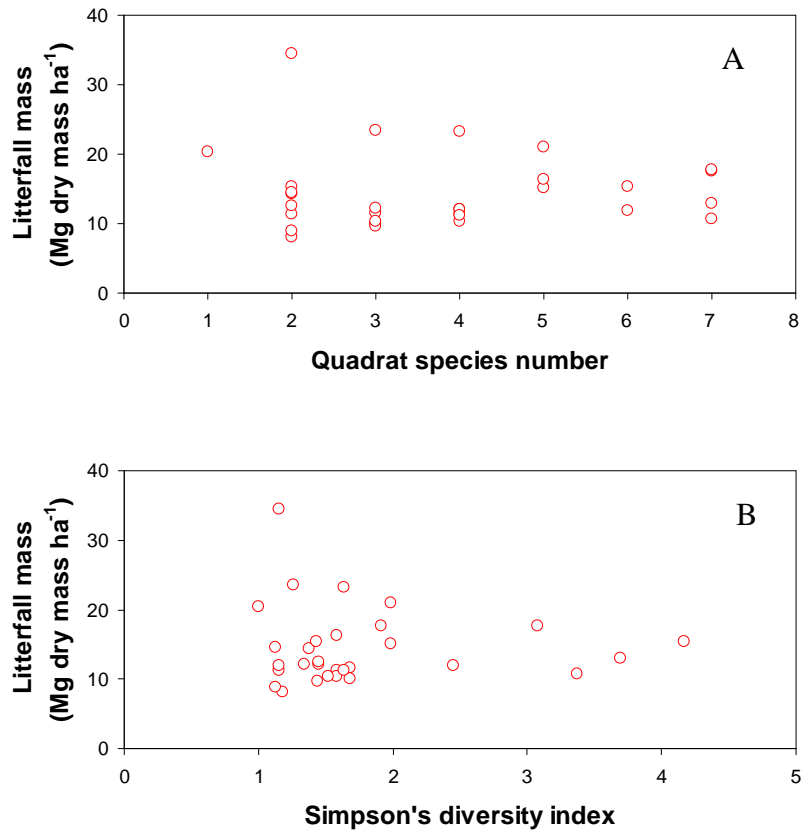


Figure 4.13 Scatter-plots of litterfall mass along a gradient of mean trap species number in monodominant forest (A); median trap species number (B); and modal trap species number (C). Each dot represents a quadrat ($n = 30$). No significant relationship was observed between litterfall mass and trap species number.

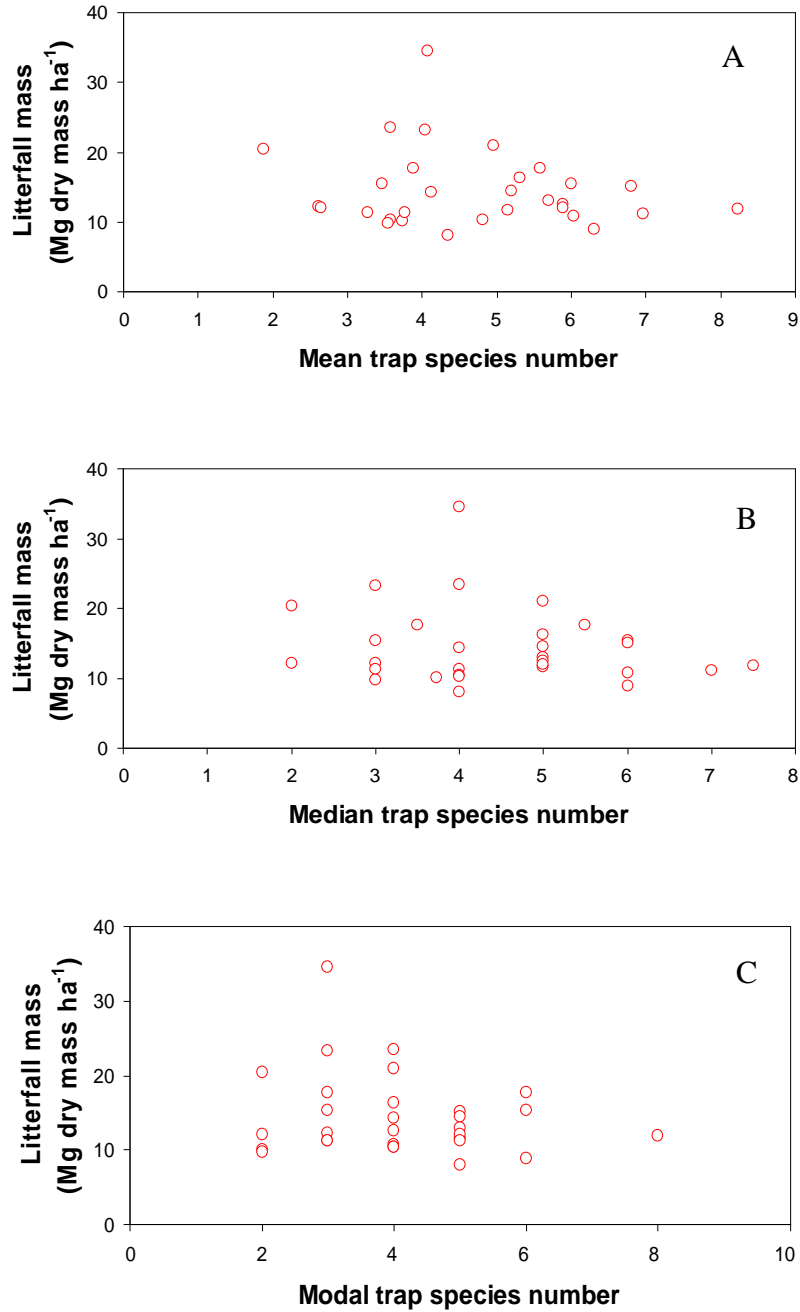


Figure 4.14 Scatter-plots of litterfall mass along a gradient of quadrat species number (A) in mixed forest; and Simpson's diversity index (B). Each circle represents a quadrat ($n = 30$). No significant relationship was observed between litterfall mass and diversity variables at quadrat level.

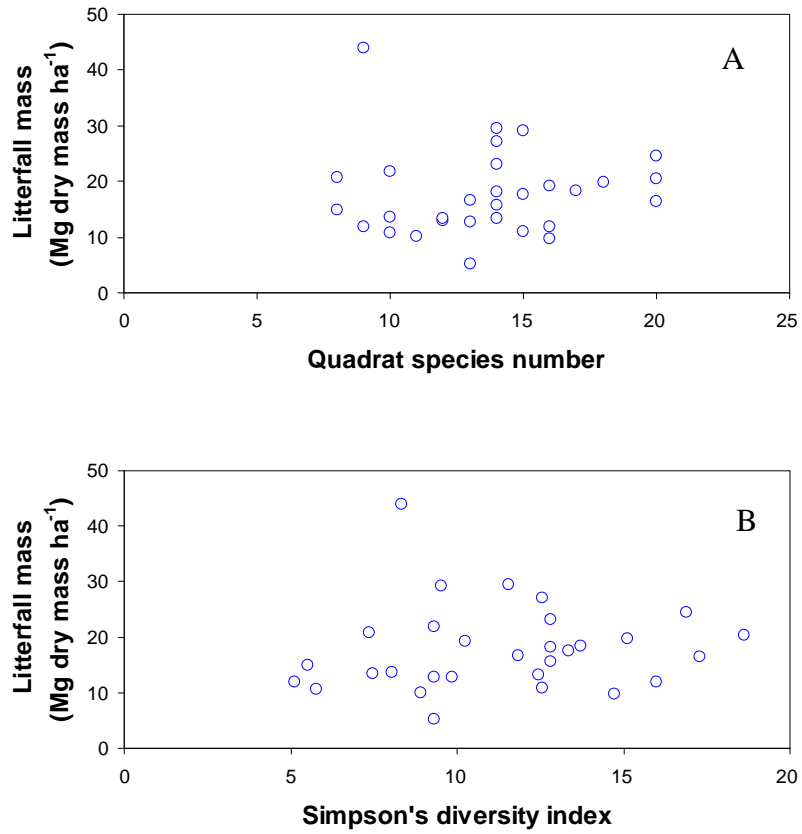
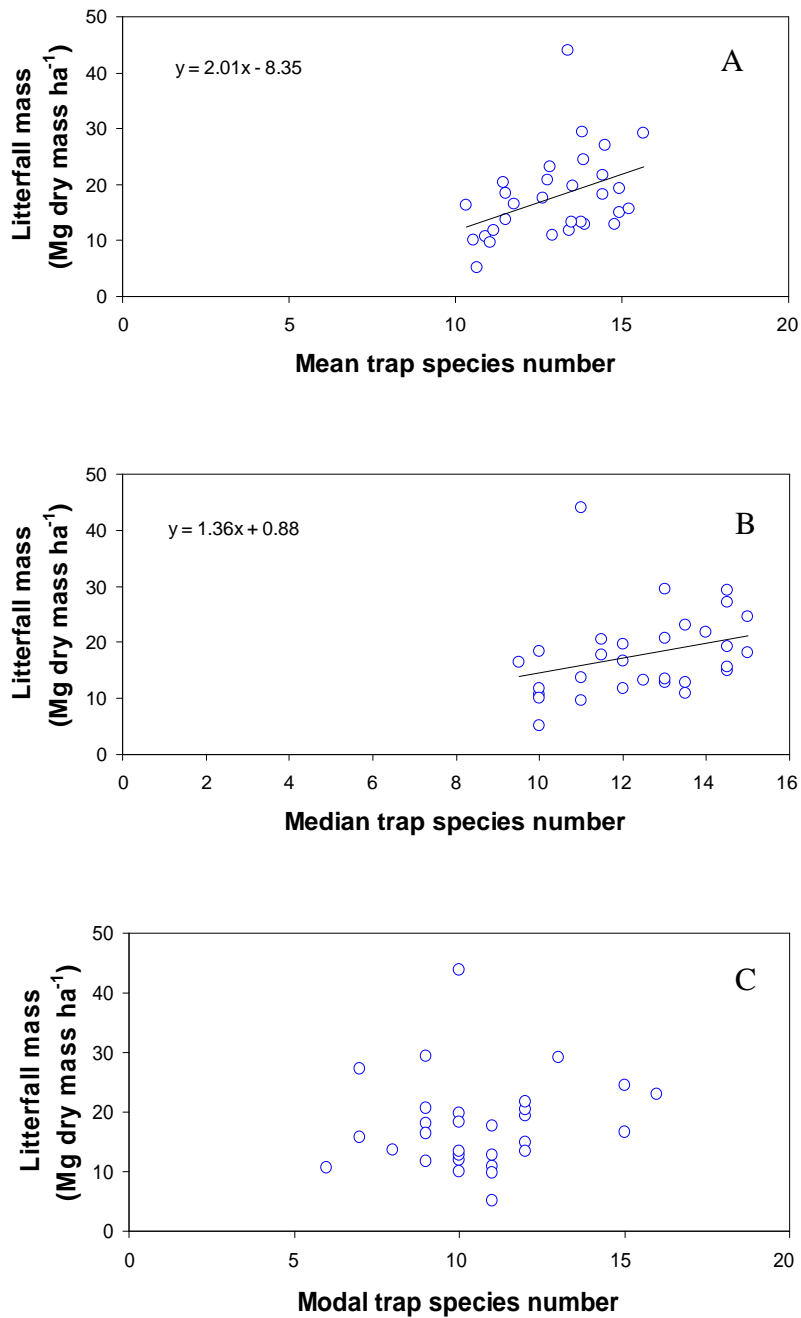


Figure 4.15 Scatter-plots of litterfall mass along a gradient of mean trap species number (A) in mixed forest; median trap species number (B); and modal trap species number (C). Each dot represents a quadrat ($n = 30$).



ANPP (\pm 95% confidence interval; $n = 3$) of the monodominant and mixed forest were 20.52 ± 3.04 Mg dry mass ha^{-1} and 21.93 ± 2.05 Mg dry mass ha^{-1} , respectively, and they were not significantly different (Fig. 4.16A). The mean of paired differences between the two forest types was 1.24 ± 2.70 Mg dry mass ha^{-1} . Pair-wise comparison of the two forest types did not show any significant difference in ANPP between the forest types (Wilcoxon signed ranks test, $n = 3$, $P = 0.285$). The scatter-plot of ANPP along the Fisher's α of all plots ($n = 6$) did not show significant relationship between ANPP and diversity index (Fig. 4.16B).

In addition, I recalculated the above-ground net primary productivity (ANPP) by adding the AGB growth derive from 2007 and 2008 census and the total litterfall productivity from April 2007 to March 2008. The values of ANPP between March 2007 and April 2008 (monodominant forest: 21.06 ± 2.06 Mg dry mass ha^{-1} ; mixed forest: 22.29 ± 1.60 Mg dry mass ha^{-1}) were not significantly different from the previous estimations.

ANPP of the monodominant and mixed forests were also not significantly correlated with all diversity variables (Fig. 4.17; 4.18; 4.19; 4.20). However, ANPP in the mixed forest increased when the mean trap species number increased (Fig. 4.17A), but the relationship was not significant (Pearson coefficient = 0.33, $P = 0.08$). Nevertheless, mean trap species number was significant ($P = 0.04$) when the effects associated to stand-level AGB, stem density and plot location were taken into consideration (Table 4.2).

Figure 4.16 Mean ANPP (n = 10 quadrats) between April 2007 and March 2008 for all six plots at the Dja Faunal Reserve (A); and scatter-plot of ANPP along Fisher's α of the monodominant forest plots (red circles) and mixed forest plots (blue circles). G1–G3 are *Gilbertiodendron*-dominated forests and M1–M3 are adjacent mixed forests. For site details see Table 4.1.

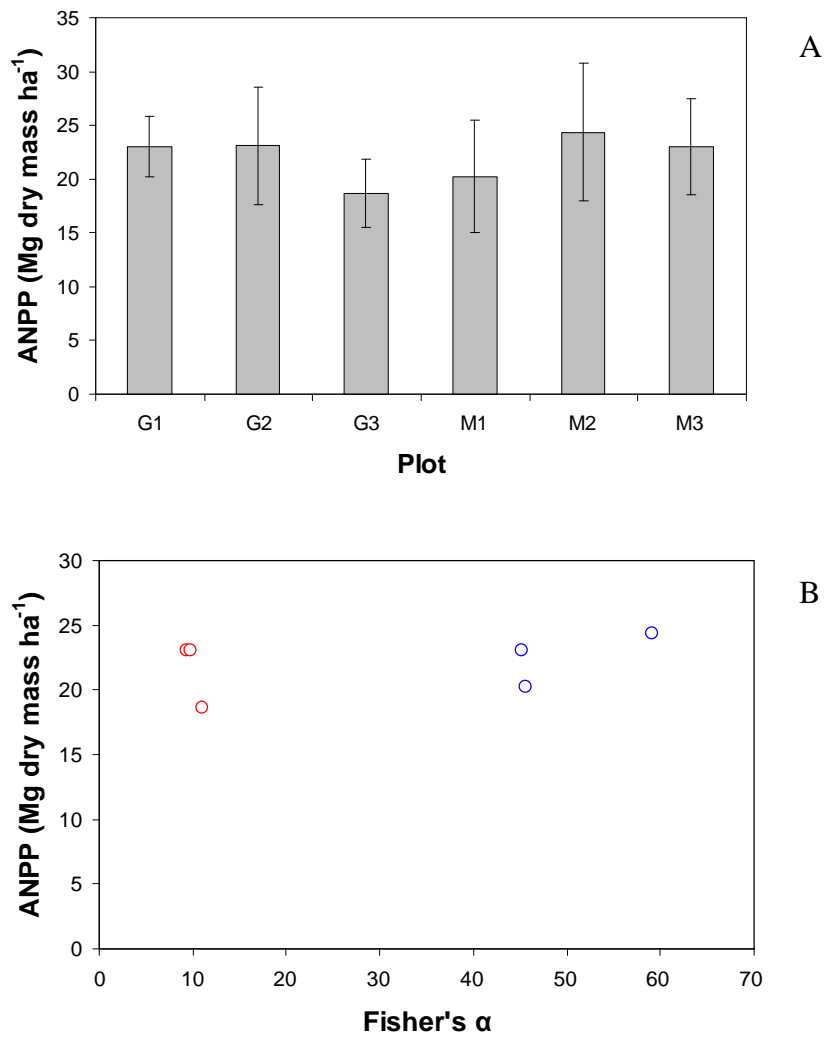


Figure 4.17 Scatter-plots of above ground net primary productivity (ANPP) along a gradient of quadrat species number in monodominant forest (A); and Simpson's diversity index (B). Each circle represents a quadrat ($n = 30$). No significant relationship was observed between ANPP and diversity variables at quadrat level.

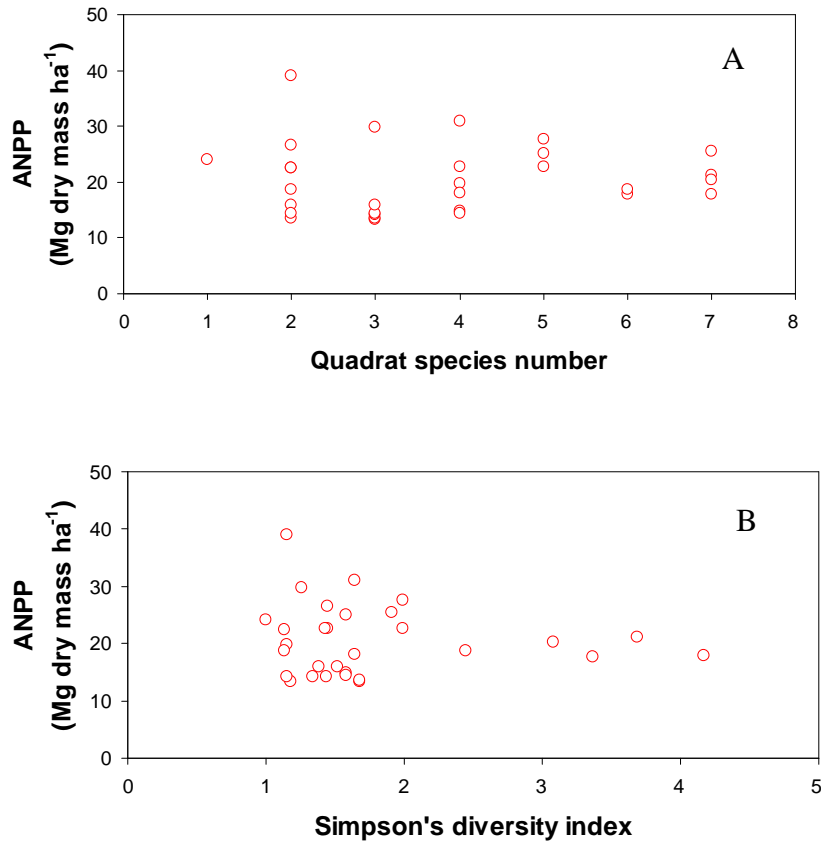


Figure 4.18 Scatter-plots of above-ground net primary productivity (ANPP) along a gradient of mean trap species number (A) in monodominant forest; median trap species number (B); and modal trap species number (C). Each dot represents a quadrat ($n = 30$). No significant relationship was observed between ANPP and trap species number.

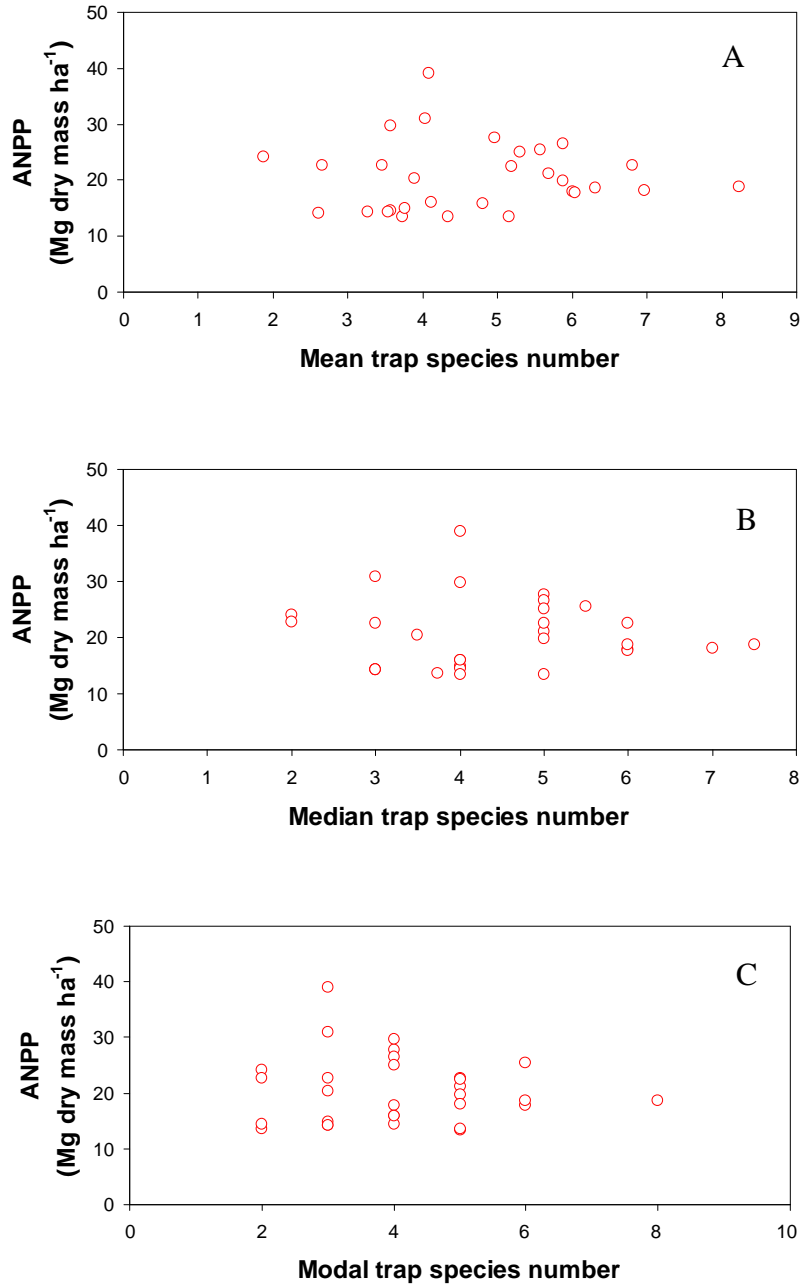


Figure 4.19 Scatter-plots of above-ground net primary productivity (ANPP) along a gradient of quadrat species number (A) in mixed forest; and Simpson's diversity index (B). Each circle represents a quadrat ($n = 30$). No significant relationship was observed between ANPP and diversity variables at quadrat level.

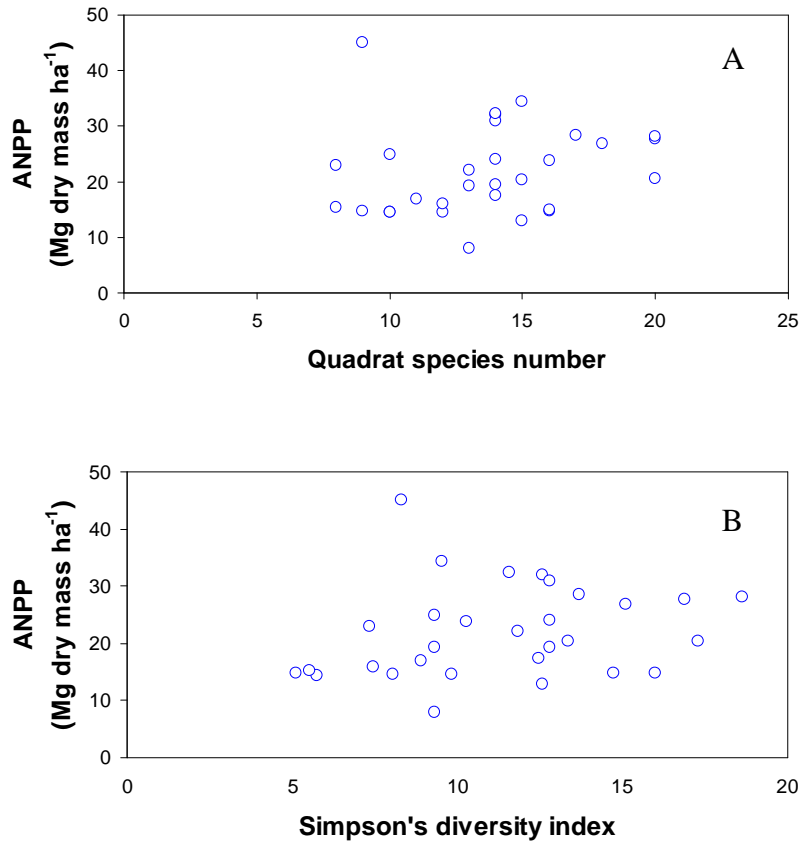
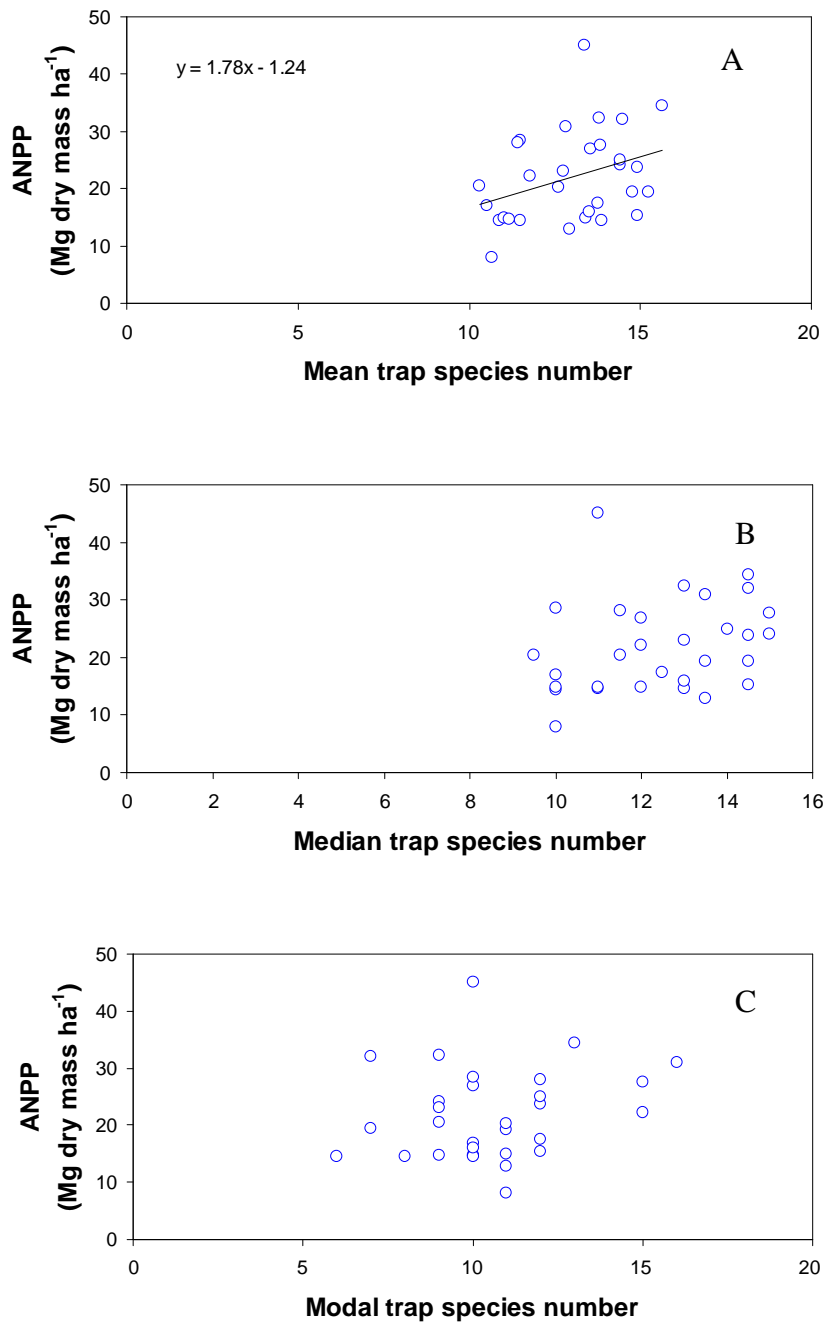


Figure 4.20 Scatter-plots of above-ground net primary productivity (ANPP) along a gradient of mean trap species number (A) in mixed forest; median trap species number (B); and modal trap species number (C). Each dot represents a quadrat ($n = 30$).



4.3.5. AGB growth of *Gilbertiodendron dewevrei*

There were only 20 species that had more than 20 individuals in the 6 ha. Among these species, those with maximum dbh ≤ 50 cm were *Angylocalyx pynaerthii*, *Centroplacus glaucinus*, *Enantia chlorantha*, *Myrianthus arboreus*, *Polyalthia suaveolens*, *Sorindeia grandifolia*, *Tabernaemontana crassa* and *Trichoscypha acuminata*. Those species with maximum dbh between 50 and 100 cm were *Anonidium mannii*, *Eriocoelum macrocerpum*, *Santiria trimera* and *Uapaca guineensis*. For those with maximum dbh ≥ 100 cm were *Carapa procera*, *Celtis zenkeri*, *Desbordesia glaucescens*, *Distemonanthus benthamianus*, *Pentaclethra macrophylla*, *Petersianthus macrocarpus*, *Uapaca acuminata* and *Uapaca paluosa*.

All species showed a positive relationship between AGB growth and dbh size ($P < 0.01$), except for *Angylocalyx pynaerthii* (Fig.4.21; 4.22; 4.23). *Gilbertiodendron dewevrei* and *Pentaclethra macrophylla* were the only species with individuals >80 cm dbh, and *Gilbertiodendron dewevrei* was the only species with individuals >100 cm dbh (Fig. 4.23). However, results of GLMs show that there is no evidence that *Gilbertiodendron dewevrei* was the most productive species: the monodominant species was only significantly more productive when compared to *Carapa procera* ($F = 4.23$, $P = 0.04$) and *Petersianthus macrocarpus* ($F = 5.55$, $P = 0.02$), whereas its AGB growth was not significantly different when compared with *Angylocalyx pynaerthii* ($F = 0.43$, $P = 0.51$), *Anonidium mannii* ($F = 1.97$, $P = 0.16$), *Celtis zenkeri* ($F = 2.33$, $P = 0.13$), *Centroplacus glaucinus* ($F = 0.44$, $P = 0.51$), *Desbordesia glaucescens* ($F = 0.90$, $P = 0.34$), *Distemonanthus benthamianus* ($F = 0.00$, $P = 0.99$), *Enantia chlorantha* ($F = 0.67$, $P = 0.42$), *Eriocoelum macrocerpum* ($F = 0.50$, $P = 0.48$), *Myrianthus arboreus* ($F = 1.48$, $P = 0.22$), *Pentaclethra macrophylla* ($F = 0.47$, $P = 0.49$), *Polyalthia suaveolens* ($F = 0.38$, $P = 0.54$), *Santiria trimera* ($F = 0.81$, $P = 0.37$), *Sorindeia grandifolia* ($F = 0.04$, $P = 0.84$), *Tabernaemontana crassa* ($F = 0.17$, $P = 0.68$), *Trichoscypha acuminata* ($F = 0.30$, $P = 0.58$), *Uapaca guineensis* ($F = 0.27$, $P = 0.61$), *Uapaca acuminata* ($F = 0.26$, $P = 0.61$) and *Uapaca paluosa* ($F = 3.69$, $P = 0.06$).

Figure 4.21 Trendlines showing the relationship between above-ground biomass (AGB) growth and diameter in breast height (dbh) for *Gilbertiodendron dewevrei* and species of maximum dbh ≤ 50 cm and had more than 20 individuals found in the 6 ha of forest plots: 1, *Gilbertiodendron dewevrei*; 2, *Polyalthia suaveolens*; 3, *Myrianthus arboreus*; 4, *Centroplocus glaucinus*; 5, *Enantia chlorantha*; 6, *Sorindeia grandifolia*; 7, *Trichoscypha acuminata*; 8, *Tabernaemontana crassa*; and 9, *Angylocalyx pynaerthii*.

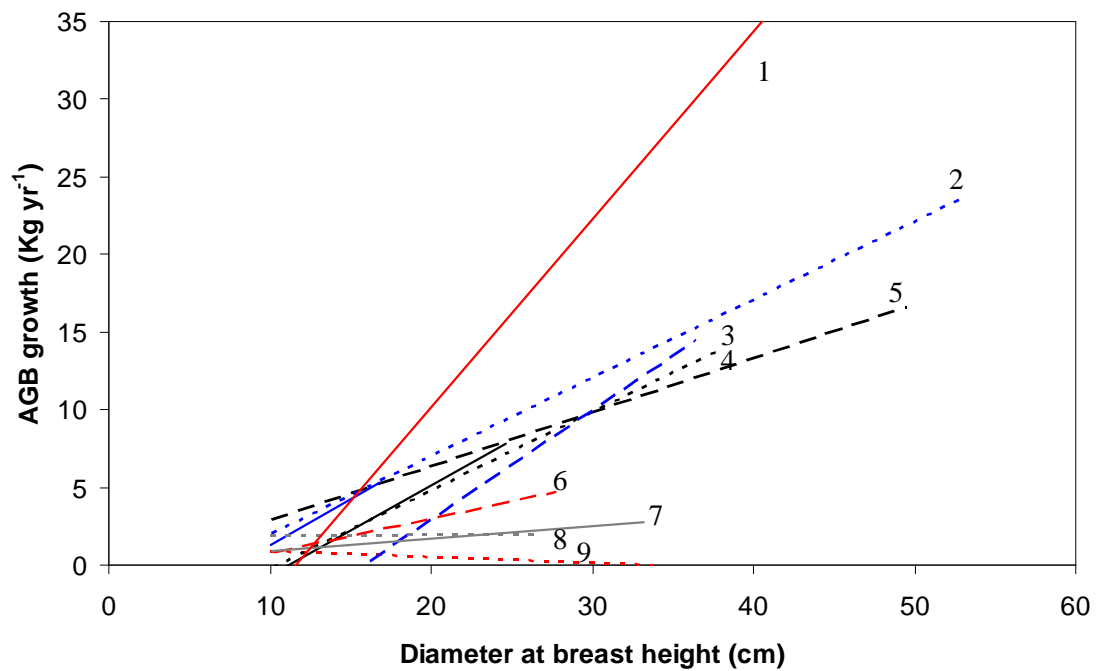


Figure 4.22 Trendlines showing the relationship between above-ground biomass (AGB) growth and diameter in breast height (dbh) for *Gilbertiodendron dewevrei* and species of maximum dbh between 50 and 100 cm and had more than 20 individuals found in the 6 ha of forest plots: 1, *Gilbertiodendron dewevrei*; 2, *Eriocoelum macrocerpum*; 3, *Santiria trimera*; 4, *Uapaca guineensis*; and 5, *Anonidium manni*.

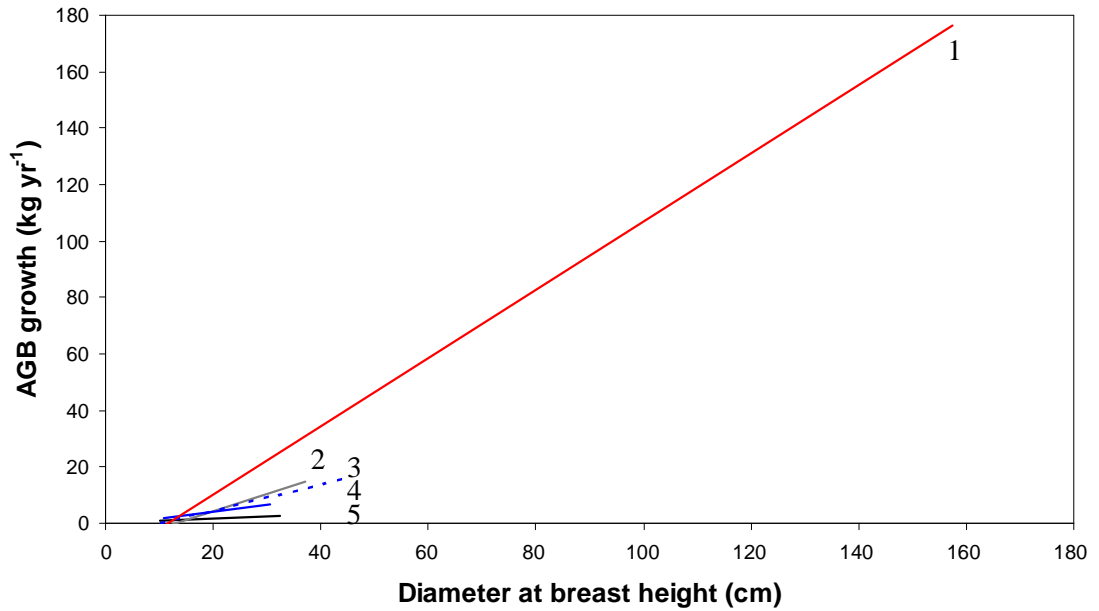
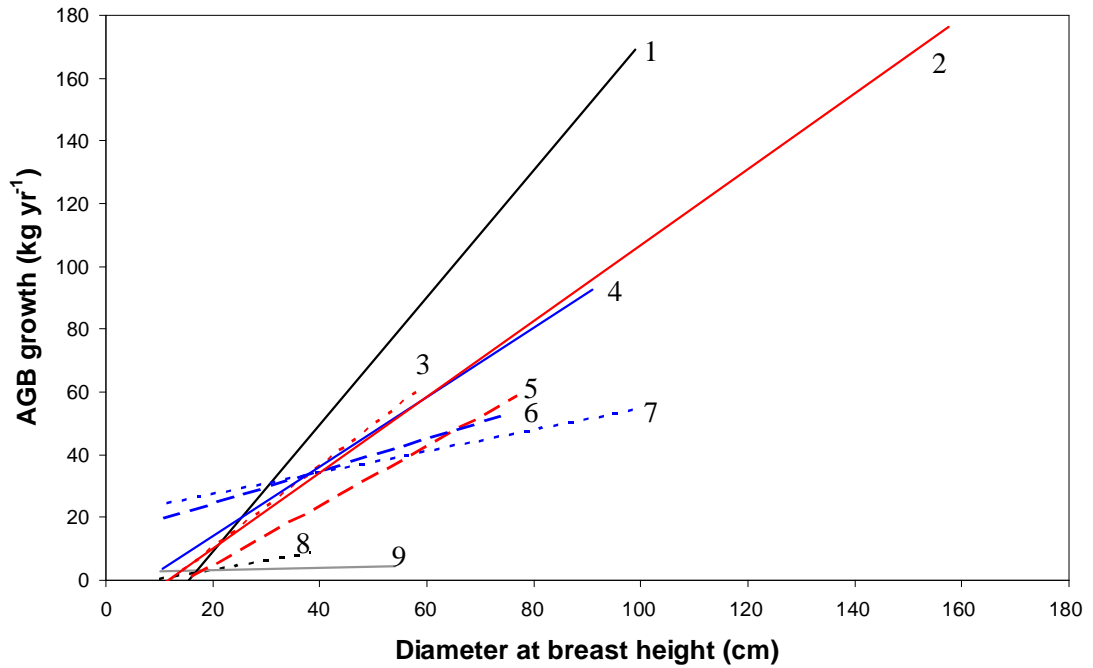


Figure 4.23 Trendlines showing the relationship between above-ground biomass (AGB) growth and diameter in breast height for *Gilbertiodendron dewevrei* and species with maximum dbh ≥ 100 cm and had more than 20 individuals found in the 6 ha of forest plots: 1, *Desbordesia glaucescens*; 2, *Gilbertiodendron dewevrei*; 3, *Distemonanthus benthamianus*; 4, *Pentaclethra macrophylla*; 5, *Petersianthus macrocarpus*; 6, *Uapaca acuminata*; 7, *Uapaca paluosa*; 8, *Carapa procera*; and 9, *Celtis zenkeri*.



4.4. Discussion

Our basal area estimates of stems ≥ 10 cm in the monodominant *Gilbertiodendron* (32.02 ± 1.54 m² ha⁻¹) and mixed forests (24.43 ± 1.93 m² ha⁻¹) were very similar to those of the study plots at Ituri in the Democratic Republic of the Congo (monodominant forests: 32.0 and 33.2 m² ha⁻¹; mixed forests: 26.2 and 26.4 m² ha⁻¹, Makana *et al.* 2004a). The estimates of the AGB and AGB growth from my monodominant plots (AGB: 552.80 ± 10.03 Mg dry mass ha⁻¹; AGB growth: 6.11 ± 2.20 Mg dry mass ha⁻¹ yr⁻¹) are similar to the AGB and AGB growth of monodominant forest at Ituri (AGB: 541.60 Mg dry mass ha⁻¹; AGB growth: 5.78 Mg dry mass ha⁻¹ yr⁻¹, Chave *et al.* 2008) whereas my mixed forest plots (AGB: 293.02 ± 49.40 Mg dry mass ha⁻¹; AGB growth: 4.48 ± 0.52 Mg dry mass ha⁻¹ yr⁻¹) had lower estimated AGB and AGB growth as compared to those of Ituri forest (AGB: 397.70 Mg dry mass ha⁻¹; AGB growth: 6.65 Mg dry mass ha⁻¹ yr⁻¹, Chave *et al.* 2008). Nevertheless, my estimates of the AGB and AGB growth are within the ranges of AGB for tropical African forests (152–736 Mg dry mass ha⁻¹, mean AGB: 404 Mg dry mass ha⁻¹, Lewis *et al.* 2009) and AGB growth for tropical forests (3.56–7.40 Mg dry mass ha⁻¹ yr⁻¹, Chave *et al.* 2008; tropical South American forests: 2.6–7.6 Mg dry mass ha⁻¹ yr⁻¹, Aragão *et al.* 2009), respectively. The estimates of ANPP of the monodominant (20.52 ± 3.04 Mg dry mass ha⁻¹ yr⁻¹) and mixed forests (21.93 ± 2.05 Mg dry mass ha⁻¹ yr⁻¹) are also within the ranges of ANPP for tropical forests (2.8–28.6 Mg dry mass ha⁻¹ yr⁻¹, Clark *et al.* 2001; tropical South American forests: 10.2–22.8 Mg dry mass ha⁻¹ yr⁻¹, Aragão *et al.* 2009).

I investigated the effect of tree species diversity on (1) basal area growth, (2) AGB growth, (3) litterfall productivity and (4) ANPP in monodominant forests dominated by *G. dewevrei* and mixed forests not dominated by a single species. Monodominant forests had greater basal area and stand-level AGB. Paired comparisons showed that the mixed forest had higher BA growth, litter productivity, and ANPP, but not AGB growth, although none were significant. However, care should be exercised in the interpretation of the data because of (1) small sample sizes (from 3 pairs of two forest types) and the assumption that the allometric

equations were representative of the reserve. Nevertheless, my findings could provide a basis for future research.

Within monodominant forest, tree species diversity had no effect on all productivity variables. In contrast, the AGB growth in the mixed forests increased with more diverse tree communities. Litterfall productivity in the mixed forest was positively related to the mean and median trap species number, which are direct measurements of species richness that contributed to the litterfall mass. The results of diversity-productivity relationship based on litterfall productivity should be more robust than those based on AGB growth. This is because the former involves direct measurements. Lastly, ANPP increased with greater mean trap species number in the mixed forest.

This study shows statistically significant effects of changes in species richness on AGB growth, litterfall productivity and ANPP in the mixed forest, thus providing empirical evidence of a positive diversity-functioning relationship in evergreen mixed forest in tropical Africa. This study also shows that *G. dewevrei* can have a dominant effect on the AGB growth, litterfall productivity and ANPP patterns; and functional traits of this dominant species can have the same or greater impact as species richness apparently does in the mixed forests. Therefore, diversity is important, but its effect can be overridden by species traits.

I investigated the diversity-productivity relationship for each forest types separately. This is because monodominant and mixed forests are two different forest systems in terms of not only species diversity and composition, but also forest dynamics. For example, the regeneration of monodominant forest involves a suite of potential positive feedbacks that may lead to a high probability of monodominance being attained (see Chapter 1). Some traits possessed by *G. dewevrei* can lead to additional and enhanced conditions that favour the establishment of greater numbers of the same species, leading to a new monodominant system (see Chapter 1).

This is a first time study to quantify litterfall productivity and ANPP of monodominant *Gilbertiodendron* forest. However, the results of my analyses may imply that the number of litterfall traps used and the one-year of litterfall data collection were not sufficient to capture the

precise litterfall production within the quadrats needed to fully understand diversity-productivity relationships. For example, the relationship was significant between AGB growth and quadrat species diversity (quadrat species richness and Simpson's diversity index) in the mixed forest. Thereafter in the same forest type, I found insignificant relationship between litterfall productivity and quadrat species diversity. But I detected a significant positive correlation between litterfall productivity and mean trap species number that measures directly the contribution of species richness to the litterfall mass. By increasing the number of litterfall traps per quadrats and prolonging litterfall data collection will predictably improve the estimations of litterfall productivity and ANPP in relation to quadrat species diversity.

Nevertheless, the results of mixed forest are largely consistent with a relationship with increasing diversity leading to an increase in stand-level productivity. The mechanism underlying the observed relationship is still unclear. Though the results indicate that the tree communities of mixed forests in the Dja Faunal Reserve achieved higher productivity with increasing diversity, their corresponding monodominant forests showed a contradictory trend. At the scale of 1 ha, the low-diversity monodominant forests were almost as productive as the mixed forests. This is likely to be because of the high density of very large trees and high initial AGB whereby wood production was higher in lower diversity due to the size-frequency distribution of the most dominant species. This is reflected in our three monodominant plots in which the AGB of *G. dewevrei* alone made up of at least 73% of the total AGB. The effect of *G. dewevrei* appears to show that the mechanism where an ecosystem function is largely determined by the presence of a species which dominate (i.e., the dominance effect) is operating in natural communities (Huston 1997).

While experimental studies are able to control for many confounding effects on diversity-functioning relationship, this study may more accurately interpret the diversity effects in a tropical forest as compared to many experimental studies because it incorporates the variability in life history and functional traits in the naturally-occurring species pool. In doing so, this study probably includes important characteristics in which experimental study designs

rarely reflect—the high-diversity species composition (100 species in <500 stems), relatively large spatial scale, non-random species assemblage and multi-trophic influence.

When interpreting the data, there is, however, a clarification I would like to make: Many studies have shown that abiotic factors associated with physiological tolerance to certain environmental conditions, such as climate and soil fertility, tend to affect productivity in tropical rain forests (Veenendaal *et al.* 1996). Thus, such factors may confound the contribution of species diversity to productivity. Simpson's diversity index is numerically analogous to resource-competition theory which predicts that species richness increases in proportion to the number of growth-limiting resources in a system where equilibrium conditions are met (Interlandi & Kilham 2001). Therefore, it may seemingly appear that I am examining the tree community response to resource availability via Simpson's diversity index. Ideally, data on climate and soil properties should be taken along the diversity gradient to obtain insight into the importance of climate and soil characteristics for productivity variation in our quadrats. But given the close proximity among all our forest plots (see Chapter 2), I assumed that the climate (i.e., rainfall) experienced by all the plots to be almost identical. Hence, climatic factors are unlikely to play an important role in our observed productivity patterns. Analysis of soils taken from my plots showed that the soil properties (soil bulk density, pH, particle size, C/N ratio, amount of P, Al, Ca, K, Mg, Na and other elements) between the two forest types and within each forest type are not significantly different (see Chapter 2). In addition, soil properties, topography and climate of the two forest types have not been shown to differ significantly at other study sites (e.g., Conway 1992; Hart 1985; Hart *et al.* 1989). Therefore, the explanation of the productivity patterns by the potential edaphic factors is also unlikely. Controlling for climate and soil effects further lends credence to the diversity effects on productivity.

My results suggest that a positive diversity-functioning relationship occurs within in the mixed forest at the site studied. However, our results also suggest that the diversity-functioning relationship may be complex with differing mechanisms being important depending upon the forest type. This study shows that productivity generally increases with more diverse tree

communities (in mixed forest), but the influence of a dominant species (i.e., dominance effect) can over-ride the diversity effect (in monodominant forest).

The results may have important implications for future impacts of global change on ecosystem function, and for improving current management practices in agroforestry and timber industry. For example, the United Nations Millennium Assessment depicts that changes in land use (e.g., the conversion of pristine tropical forests to logged forests) may be the main driver for the alteration of biodiversity of tropical forests in 2050 (Convention on Biological Diversity, <http://www.biodiv.org>). Therefore, the loss of α -diversity resulted from selective logging may be one of the mechanisms that constrain the tropical forest ecosystem function. Because one of the consequences of tree species loss may be the reduction of tree biomass productivity (see Bunker *et al.* 2005), understanding how changes in tree species diversity affect the timber harvest remains an important focus of agroforestry and timber forestry. This study predicts that plant productivity is likely to be more affected by the loss of species in high-diversity communities than in equivalent low-diversity communities. Thus, it is important to establish and maintain tree species rich communities to enhance long-term productivity.

4.5. Summary

- The monodominant forests had a higher AGB and basal area as compared with the mixed forests.
- BA growth, AGB growth, litter productivity and ANPP of the monodominant and mixed forests did not appear to be different.
- In the monodominant forest, there were no significant relationships between AGB growth and quadrat species number, and between AGB growth and Simpson's diversity index; litterfall productivity and ANPP were not significantly correlated with mean, median and modal trap species number.
- In the mixed forest, there were positive relationships between AGB growth and quadrat species number; between AGB growth and Simpson's diversity index; between litterfall

productivity and mean and median trap species number; and between ANPP and mean trap species number.

- Although there is a diversity effect in the mixed forest, individual species can be important; the dominant *G. dewevrei* influences the AGB growth, litterfall productivity and ANPP in the monodominant forest.

5. Litterfall phenological observations: biomass allocation and variability in litterfall productivity in two lowland forests with contrasting tree diversity

5.1. Introduction

Tropical landscapes worldwide are being rapidly degraded by human activities. The rate of species loss in tropical systems caused by the overexploitation of natural resources and habitat conversion is acute, given the high species richness of these habitats (Bradshaw *et al.* 2009). A better understanding of the changes in these tropical systems and their effects is much needed if ecologists are to add to the knowledge essential for the maintenance of the important ecosystem functions provided by these systems. One way to achieve this is to demonstrate how biodiversity stabilizes the ecological processes of these natural systems. Furthermore, the nexus between diversity and stability may be one way of explaining diversity-productivity relationships within these systems.

However, it is not a straightforward task to understand the effects of diversity on stability. This is because the concept of stability is complex. Stability can take on different definitions depending on the ecosystem properties of interest; and different types of stability can result in different diversity-stability relationships (Ives & Carpenter 2007). For example, in a system with a stable equilibrium, the rate of secondary extinction caused by the removal of the most common species and the rate of secondary extinction caused by the introduction of an invasive species may be different. Furthermore, understanding the effects of diversity on stability also requires knowledge of how species interact with their surrounding biotic factors (e.g., other species) and how each species is affected by the abiotics factors (e.g., environmental drivers). Here I focus on the concept of stability that involves a measure of temporal variability of the ecological processes. More precisely, this chapter deals with the stability that measures the variability in litterfall mass over one year in tropical forests.

Diversity-stability relationships might arise due to a diversity of species possessing different functional response traits which act as ‘insurance’ in carrying out ecological processes

when the ecosystem is subjected to disturbance. Several recent empirical studies of diversity-stability relationships have shown that greater stability of the ecosystem properties is achieved with increasing diversity. There were 16 diversity-stability studies (field experiments), published since 1990 (reviewed by Ives & Carpenter (2007)) that tested the influence of diversity on temporal stability of biological responses to perturbations; 12 of the 16 studies reported positive relationships between diversity and temporal stability of biomass production and only two showed negative relationships. However, these temporal stability studies should be interpreted with caution because there is a strong bias towards temperate grasslands (i.e., six of the 12 studies) and only one report studied tree-dominated system (a temperate forest). In addition, most of the diversity-stability studies were performed in a highly-controlled environment whereby the effects of the changes in diversity were being investigated with all other variables being equal to control for confounding effects. However, there is a need for complementary studies to be carried out in a realistic environment (i.e., field-based studies) to test these experimental conclusions. Field-based studies are able to incorporate features such as non-random species assemblage and multi-trophic influence that are rarely reflected in experimental studies.

Although the notion that diversity enhances temporal stability in terms of biomass productivity has been well supported by mathematics models (e.g., Valone & Barber 2008), manipulative diversity experiments in microcosms (e.g., Morin & McGrady-Steed 2004) and temperate grasslands (e.g., Tilman 2006), to my knowledge no studies have attempted to explore such relationships within a tropical forest. In this chapter, I discuss the temporal variability in litterfall mass from African tropical forests that vary in diversity. Litterfall is a measure of leaf, fruit, flower and fine wood production, and accounts for 53–78% of total ANPP (Clark *et al.* 2001). Understanding the variability of litterfall is important because litterfall phenology influences forest dynamics by contributing to the transfer of organic matter from plants to soil fauna and soil organic matter pools (Vitousek & Sanford 1986).

My study site consisted of permanent sample plots within two forest types with contrasting tree diversity (i.e., the monodominant *Gilbertiodendron dewevrei* forest and its

adjacent mixed forest) where I compared the temporal variability of litterfall between the two forest types over one year. I also tested the relationship between tree species diversity and the temporal variability of litterfall within each forest type. The biodiversity-stability theory assumes equilibrium (Thompson *et al.* 2005). Since the vegetation of the study sites has experienced no obvious recent disturbance, I assumed that the biomass and tree species richness of my focal quadrats are likely to be at or near equilibrium. I argue that the changes in temporal variability in litterfall biomass in response to diversity were not due to transient dynamics because the above-ground biomass of the trees did not drastically change over the one year of study (i.e., no recruitment and mortality observed in the focal quadrats) and the tree species composition did not shift over the length of the litterfall collections. The tree species richness did not change within the quadrats over the year of study and therefore can be used to explore the relationship between diversity and the stability of the ecosystem functioning.

Based on the litterfall data from the two distinct forest systems, I aimed to answer the following questions:

- (1) Is the amplitude of the annual variation in litterfall higher in the low-diversity monodominant forest than the high-diversity mixed forest?
- (2) Are the leaf litterfall, flowering and fruiting phenology patterns synchronized between the two forest types?
- (3) Is the biomass allocation (leaves, flowers, fruits etc.) different between the two forest types?

5.2. Methods

I conducted this study in the monodominant *Gilbertiodendron* forest and its adjacent mixed forest at the Dja Faunal Reserve (for description of the study sites, see Chapter 2). Soils in the two forest types are clay-rich, acidic, silty oxisols (see Chapter 2). Physical and chemical soil properties – soil bulk density, pH, particle size, C and N contents, C/N ratio, concentrations of labile, organic and inorganic P, and other trace elements such as Al, B, Ba, Ca, Co, Cr, Cu, Fe, K, Mn, Mo, Na, Ni, Se, Si, Sr, Ti, V and Zn – along a depth gradient (0–2 m) were not

significantly different between the monodominant and mixed forests (for description of soil analyses, see Chapter 2).

5.2.1. Tree survey and litterfall collection

The sampling design used corresponds to the previous studies described in Chapter 4 and includes three study sites each in monodominant forest and the adjacent mixed forest. Therefore, my study included a total of 6 plots of 1 ha each.

Each plot was subdivided into 25 quadrats (each 20 m × 20 m), in which each individual tree with diameter at breast height (dbh) ≥ 10 cm or above buttress was identified. Then within each plot, I randomly chose 10 quadrats, and within each selected quadrat, I installed three standing litterfall traps (0.5 m × 0.5 m, 1 mm mesh; 1.0 m above the ground) and three ground traps (0.5 m × 0.5 m, no mesh; on the ground). The total area covered by the 180 standing traps over 60 quadrats was 45 m². All traps were randomly placed at least 5 m away from the perimeter of the quadrats to minimize the influence of the adjacent quadrats (i.e., edge effect) (Wardle & Zackrisson 2005). I combined materials collected in the traps from each quadrat into a single sample and therefore I had 60 samples per collection date. Litter was collected every two weeks from April 2007 to March 2008. Litter collected from the standing traps was sorted into the following categories: leaves, woody litter (wood diameter <1 cm), flowers, fruits and seeds. I only collected fine wood debris (wood diameter ≥ 1 cm to 10 cm) from the ground traps. The oven-dried weight of total litterfall (expressed in Mg dry mass ha⁻¹), derived from each of 10 quadrats in each of the six plots was used (1) to determine if there is a difference in the amplitude of the annual variation (i.e., variability) of litterfall mass between the monodominant and mixed forests and (2) to determine if the amplitude of the annual variation of litterfall mass correlates with species diversity at a small-scale level within each forest type.

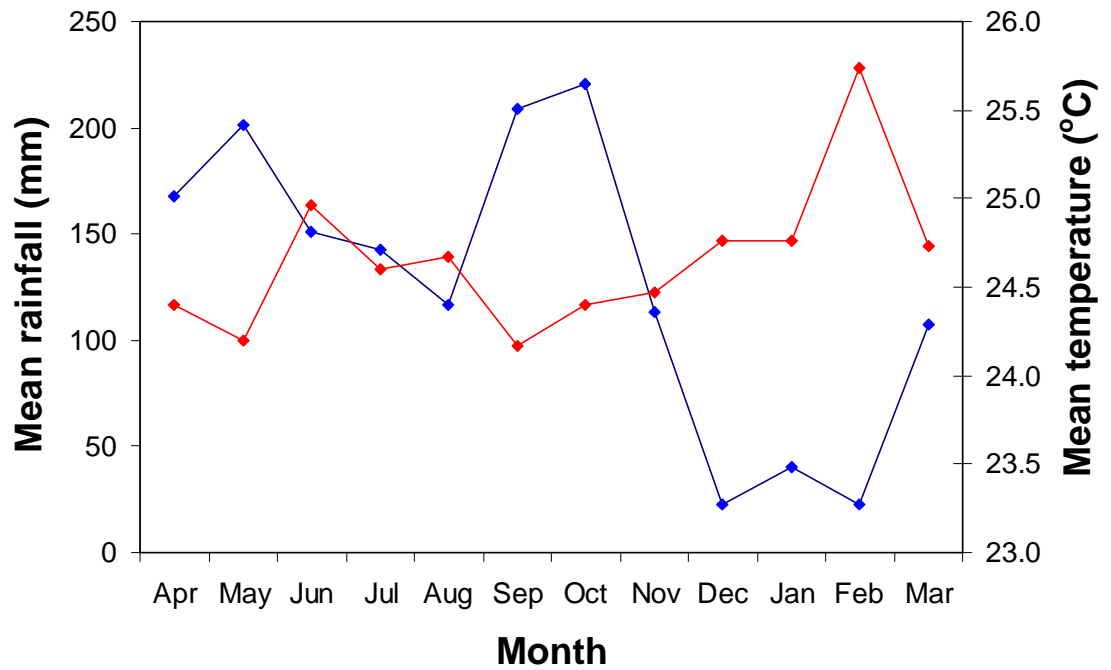
5.2.2. Data analyses on biomass allocation and temporal patterns of litterfall

To compare the absolute amounts of litterfall per litter category between the two forest types, mean litterfall productivity rates were calculated (expressed in Mg dry mass ha⁻¹) for each category for the monodominant and mixed forests (n = 3 pairs). Further, litter data per category in each forest type, initially as absolute rates, were converted to percentages of the annual total litterfall and then averaged (n = 3). This enables the comparison of relative amount of litterfall per category (i.e., biomass allocation) between the two forest types.

Temporal patterns of total litterfall and each litter category were analyzed with a one-way ANOVA using general linear model (GLM) procedure, in which litterfall category or total litterfall was the dependent variable, collection date was the fixed factor and site was the random factor (Zalamea & González 2008). When the effect of collection date was significant, I employed the Least-Significant Difference (LSD) post hoc test to determine the differences among specific collections so as to identify the number of litterfall peaks (Zalamea & González 2008). In order to identify if there were any peaks at the start (April 2007) and at the end (March 2008) of the study duration, I looped the start and the end of the study period for the LSD post hoc test. A peak is defined if the value spanning one to several collections being significantly different ($P < 0.05$) from those of the adjacent collections.

Climatic data (Fig. 5.1) of precipitation (mm) and temperature (°C) for the study duration (April 2007–March 2008) were obtained from three meteorological stations near the reserve (see Chapter 2 for the details of these meteorological stations). I averaged the data from these meteorological stations for the estimations of monthly precipitation and monthly temperature. Correlation analyses along all collection dates using Spearman's rank coefficient were carried out between litter categories of each forest type and the climatic variables (precipitation and temperature).

Figure 5.1 Averaged monthly rainfall (blue line) and temperature (red line) patterns in the Dja Faunal Reserve from April 2007 to March 2008. Data were collected from three meteorological stations near the reserve.



5.2.3. Data analyses on diversity effects

To determine the relationship between species diversity and functioning, I counted the number of tree species identified and also calculated the Simpson's diversity index for each of 60 quadrats (for calculation of Simpson's diversity index, see Chapter 4). Previous studies have found that species evenness is likely to be among the main determinants in various ecosystem functions (e.g., Polley *et al.* 2003). Hence, I also tested the effect of species evenness, another component of diversity (for calculation of species evenness, see Chapter 4).

Since the total area of the standing traps covered only a small proportion of a quadrat (approximately 0.2 %), I predicted that the observed species richness and Simpson's diversity index at quadrat level might not truly reflect the plant diversity that contributed to litterfall mass. Thus, I developed measures of relative species richness (hereafter mean, median and modal trap species number) to describe the α -diversity surrounding the traps (for calculations of mean, median and modal trap species number, see Chapter 4). The mean, median and modal trap species number included liana species and matched more closely my *a priori* objectives. Although the mean trap species number and median trap species number in the monodominant forest were significantly correlated with the observed quadrat species number (Fig. 5.2, A & B) and Simpson's diversity index (Fig. 5.3, A & B), I included them all in my statistical analyses to explore if mean and median trap species number have greater explanatory power to changes in the litterfall.

Figure 5.2 Scatterplots of quadrat species number along the gradient of mean (A), median (B) and modal (C) trap species number. Red circles represent the monodominant forest quadrats and blue circles are the mixed forest quadrats. Traps could have more species than quadrats due to the input of leaves from plants <10 cm dbh and lianes.

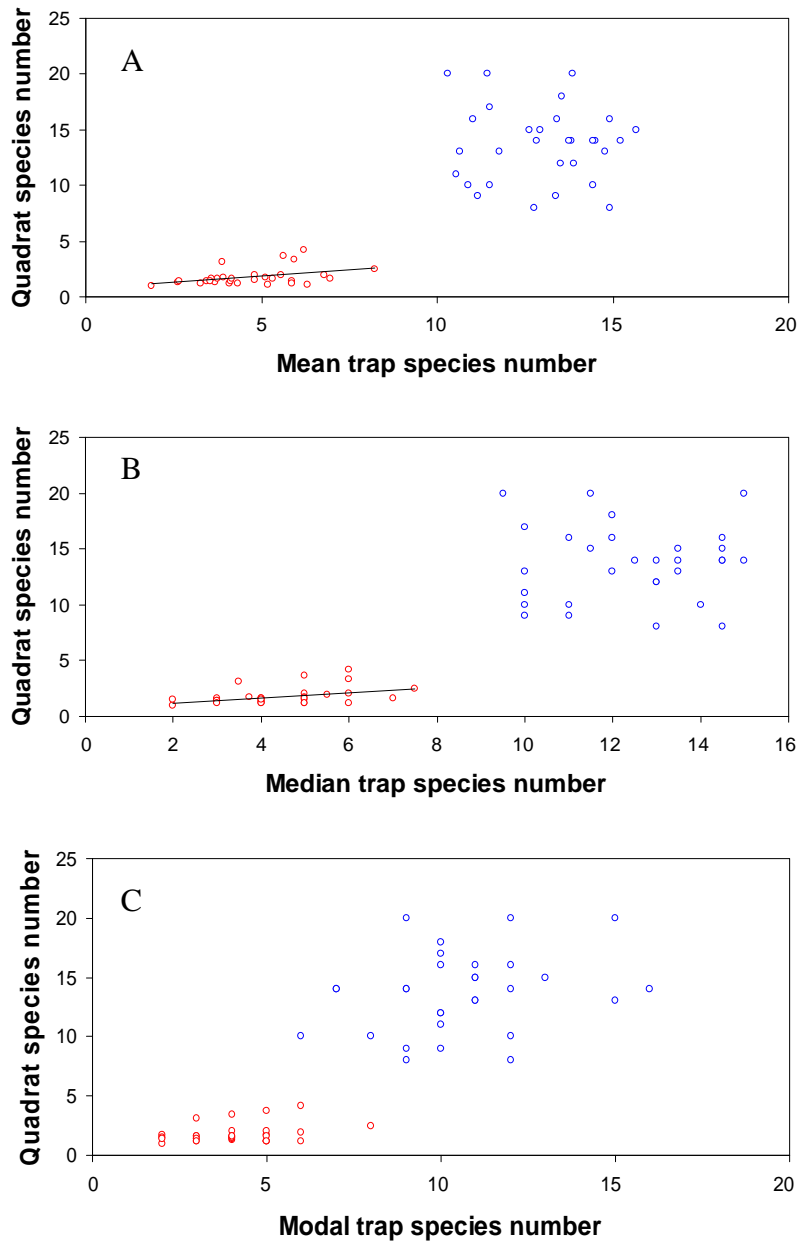
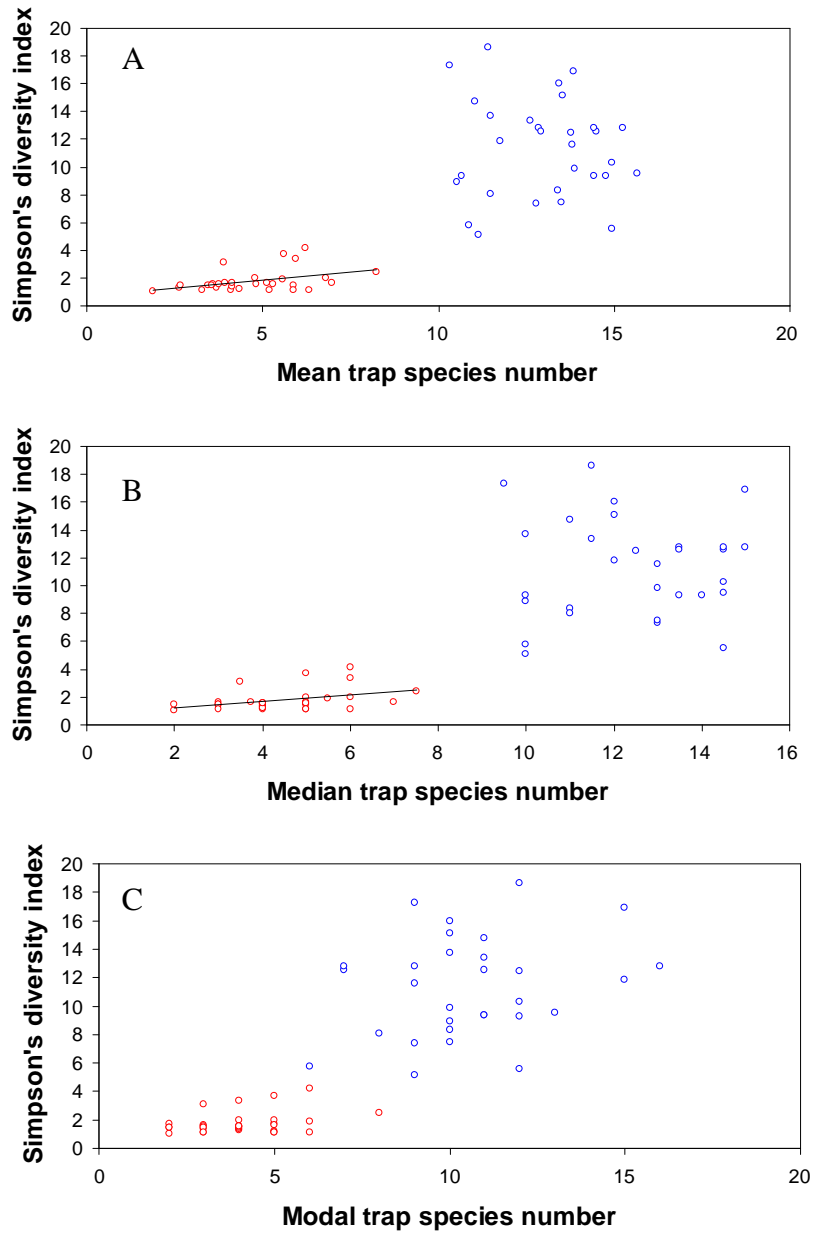


Figure 5.3 Scatterplots of Simpson's diversity index along the gradient of mean (A), median (B) and modal (C) trap species number. Red circles represent the monodominant forest quadrats and blue circles are the mixed forest quadrats.



Since the monodominant and mixed forests are two distinct systems (see Chapter 4 for details), I analysed each forest type separately. To explore the relationship between temporal variability of total litterfall mass and species diversity of a community within each forest type, I calculated the standard deviation (SD) of logarithmically-transformed litterfall mass for each of 60 quadrats over 26 collection dates. Because the means and variances of my litterfall data used for evaluating effects of species richness on variability showed significant positive correlations, I logarithmically transformed the data to minimize potential artefacts arising from the correlations between means and variances of litterfall mass (Cottingham *et al.* 2001; McGrady-Steed *et al.* 1997). I chose SD (following Morin & McGrady-Steed 2004) instead of coefficient of variation (CV) as my measure of variability because lower values of the latter may be an artefact of the higher relative litterfall mass (i.e., 'statistical averaging') and not because of lower variance (see Doak *et al.* 1998; Steiner *et al.* 2005).

For each forest type, I calculated the Pearson's correlations of temporal variation in litterfall over time with quadrat species number, Simpson's diversity index, species evenness, and mean, median and modal trap species number. I checked and then log-transformed the data to ensure normality, and used the Spearman rank correlation test where normality of data was not improved. When the effect of a diversity parameter (i.e., quadrat species number, Simpson's diversity index, quadrat species evenness or trap species number) was significant, I performed further statistical controls to separate any potential spatial effect (i.e., variation due to plot location). Therefore, to test the effects attributable to diversity and to test for the dependence of residual variation on plot location in litterfall variability, I used GLM analyses of covariance with type III sums of squares, in which the plot location was the random factor and litterfall mass SD was the dependent variable. All tests were performed with SPSS (2006). Multiple tests of significance were subjected to Bonferroni correction procedure (Rice 1989). Otherwise, significance was established for P values <0.05 . Then I pooled the data from both forest types to further explore the diversity-stability relationship by fitting a regression model with the data.

Although my study design did not differentiate if the differences in variability of litterfall were caused by changes in the number of species *per se*, or by the effects of particular

species (i.e., 'selection effect'), it is possible to argue that the quadrat communities of identical species richness had different species combinations and thus avoiding the confounding diversity effects with species composition. Nevertheless, I checked if the changes in temporal variability can still be explained by diversity with statistical control for the abundance of species that had more than three individuals found in the 30 quadrats. I used partial correlation analysis to assess whether the significant measures of diversity retained from the GLM independently affect temporal variations by statistically controlling for the effect of variation in abundance of a particular species.

5.3. Results

5.3.1. Total litterfall and biomass allocation

The 3 ha of mixed forest plots had higher species richness than the three ha of monodominant forest plots with total tree species of 198 and 71, respectively (see Chapter 3). Total litterfall dry production (including fine wood; $\pm 95\%$ confidence interval, $n = 3$) collected over a year was 14.54 ± 3.13 Mg dry mass ha^{-1} in the monodominant forest plots and 17.77 ± 1.99 Mg dry mass ha^{-1} in the mixed forest plots. The 95 % confidence intervals of both forest types overlapped (Fig. 5.4A). However, the mixed forests had consistently higher total litterfall dry production than the monodominant forests in the pair-wise comparison. The mean of paired differences between the two forest types was 3.23 ± 1.27 Mg dry mass ha^{-1} (Fig. 5.5A). Nevertheless, the differences in total litter dry mass between the two forest types remained insignificant (Wilcoxon signed rank test, $n = 3$, $P = 0.109$).

There was a difference in the biomass produced for the various litterfall categories between the two forest types. More specifically, the average production of leaves and woody litter ($n = 3$) was significantly higher in the mixed forests (Fig. 5.4A). These patterns were also confirmed in the pair-wise comparison when the leaf litterfall dry mass of the mixed forests was consistently higher than that of the monodominant forests (mean of paired differences in leaf litterfall dry mass is 3.28 ± 1.31 Mg dry mass ha^{-1} and that of woody litterfall dry mass is $1.84 \pm$

0.74 Mg dry mass ha⁻¹ (Fig. 5.5, A & B). On average, monodominant forests produced more flowers, fruits and seeds (Fig. 5.4A) but variation among the three plots of monodominant forests was large (Fig. 5.4, B & C). The mean of paired differences in flower litterfall dry mass between the two forest types was 0.96 ± 1.16 Mg dry mass ha⁻¹ and the mean of paired differences in fruit/seed litterfall dry mass was 1.92 ± 2.02 Mg dry mass ha⁻¹ (Fig. 5.5, A & B).

The proportional biomass allocations among the leaf, flower and fruit/seed litterfall categories were not significantly different between the two forest types, except that the mixed forests had higher biomass allocation to woody litter (Fig. 5.4B). On average, 45% and 54% of the litterfall biomass in monodominant forests and mixed forests, respectively, were made up of leaf litter but the biomass allocation to leaves was not significantly different between the two forest types (Fig. 5.4B). Between forest types, the mean of paired differences in proportion of litterfall mass allocated to leaf and mean of paired differences in proportion to woody litter were 0.10 ± 0.09 and 0.07 ± 0.05 , respectively.

Although monodominant forests allocated more litterfall mass to flowers (mean of paired differences between forest types = 0.07 ± 0.07) and fruit/seeds (mean of paired differences between forest types = 0.13 ± 0.12) in the year of monitoring, the variability in the biomass allocation to the reproductive structures was high (Fig. 5.4B). This may be because the three monodominant forest plots experienced different degrees of masting during the period of litterfall phenology surveys. In addition, *G. dewevrei* does not reproduce annually. Based on the three replicates of each forest types, the variability in the biomass produced in the form of leaves, reproductive structures and woody litter was higher among the monodominant forests (Fig. 5.4C). Further, the total litterfall mass among the monodominant forests also appeared to have higher variability (Fig. 5.4C). When the biomass allocation patterns among the monodominant forest plots were examined, the plot with the highest proportion of leaf biomass had also exhibited the lowest degree of masting, with the lowest proportions of flower and fruit/seed mass produced (Fig. 5.6).

Figure 5.4 Mean absolute litterfall production, expressed in Mg dry mass ha⁻¹ (A), mean relative litterfall production (B) and litterfall production standard deviation (C) per litter category in monodominant (grey bars) and mixed (white bars) forests. The error bars represent 95% confidence interval (n = 3).

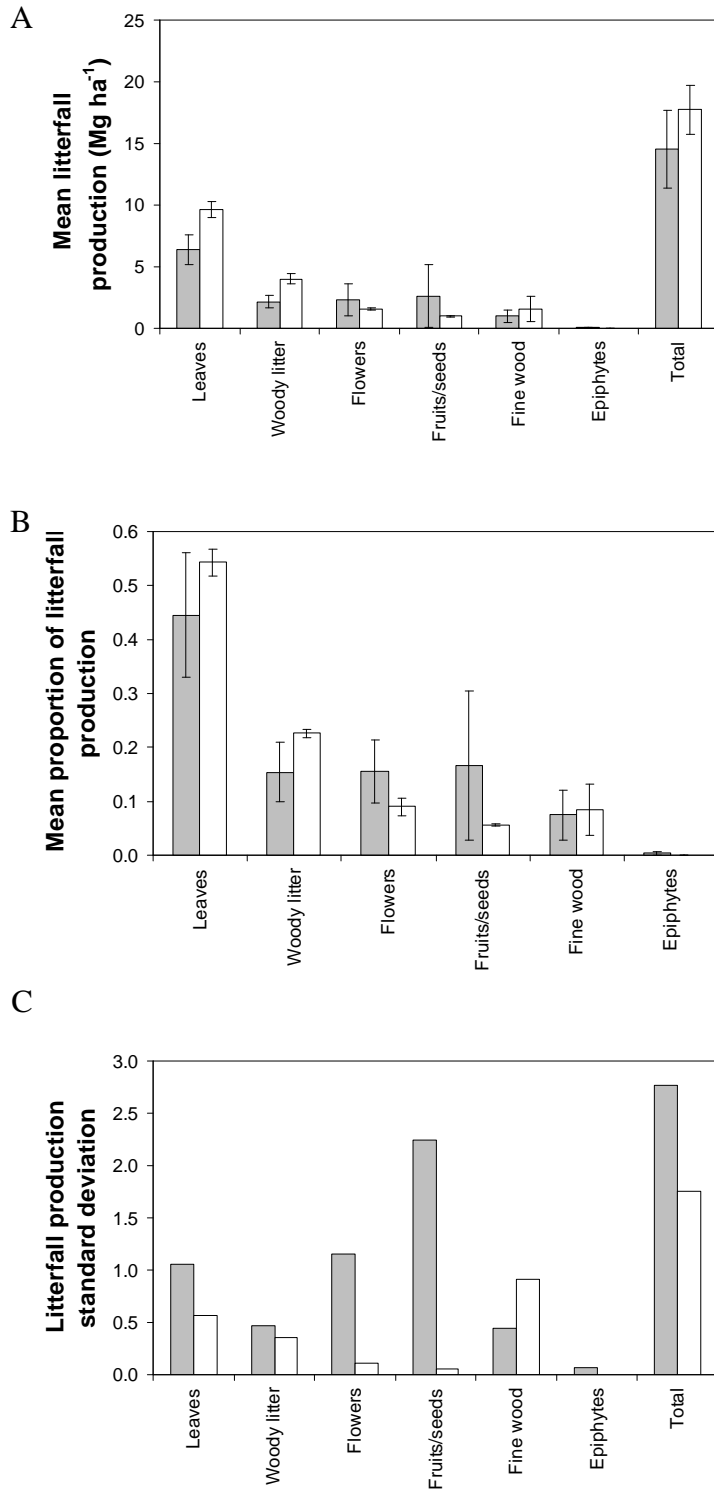


Figure 5.5 Absolute amounts of litterfall per category in each monodominant (A) and mixed (B) forest plots. Each colour of the bar represents a different study site. The same colour bars across the two forest types represent the two adjacent plots of the same site.

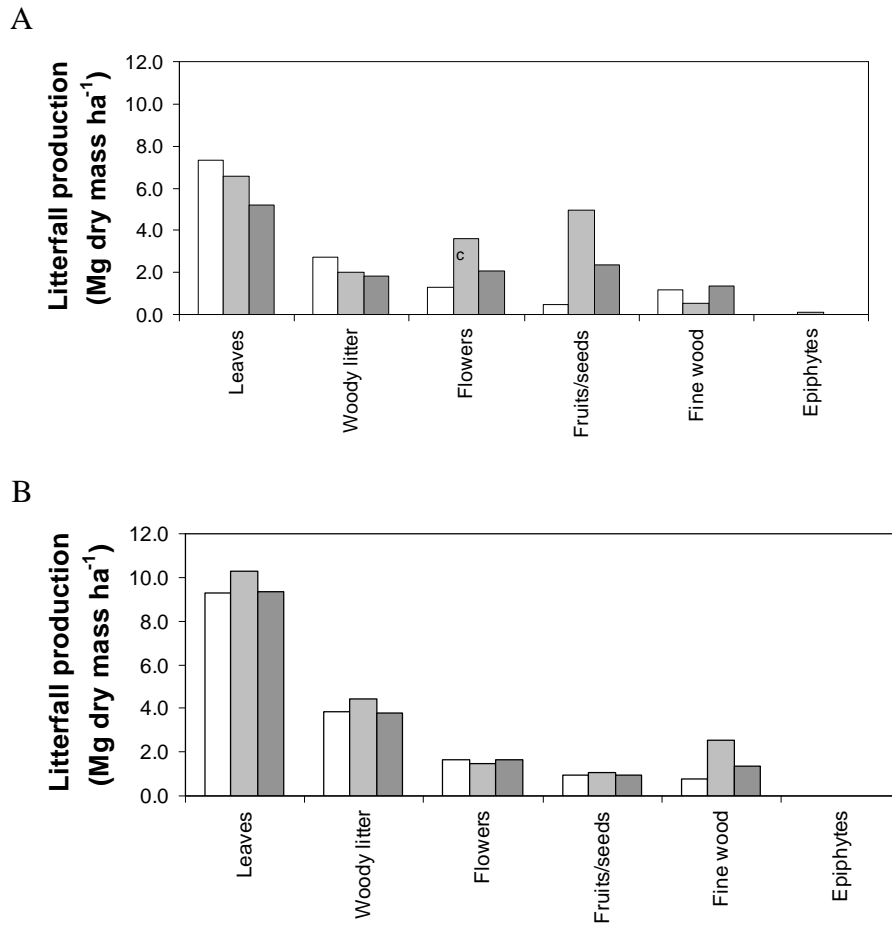
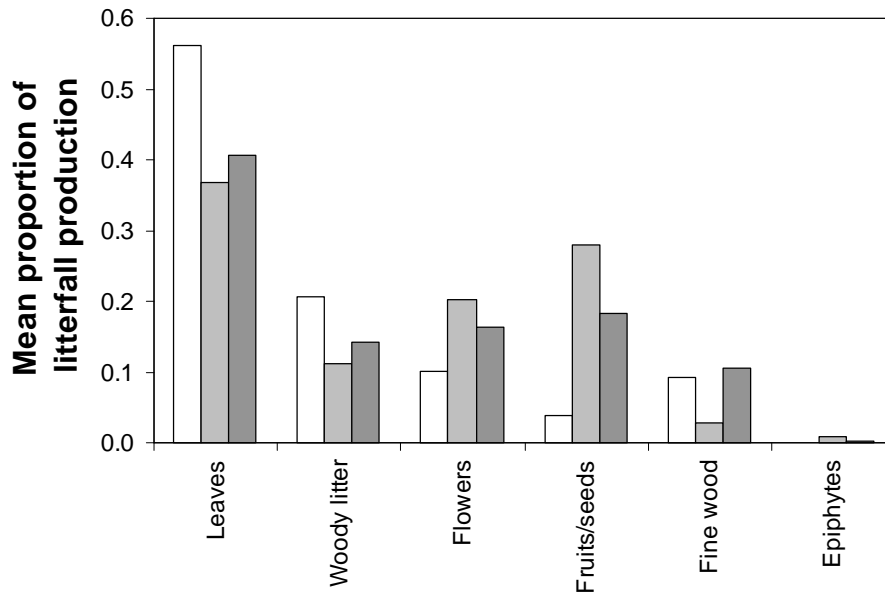
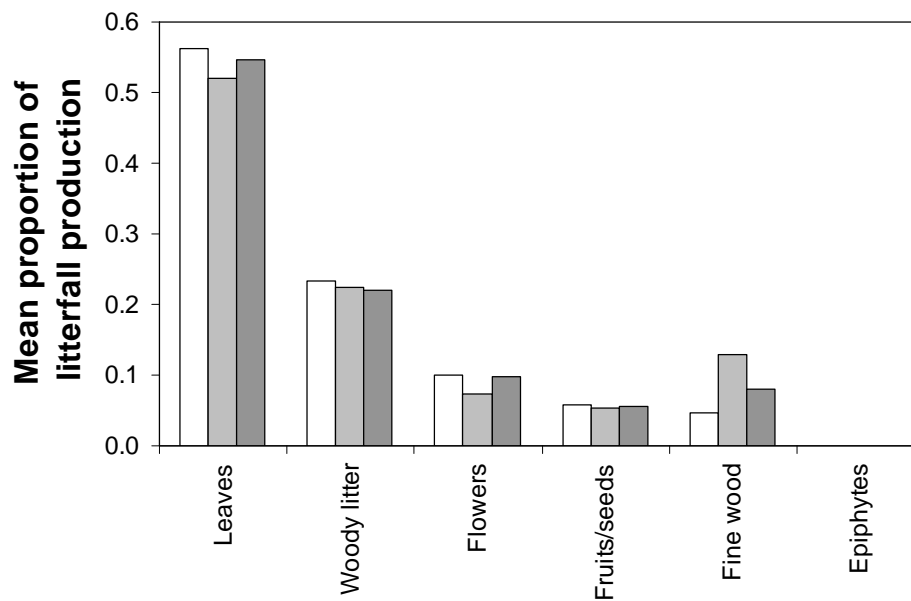


Figure 5.6 Relative amounts of litterfall per category in each monodominant (A) and mixed (B) forest plots. Each colour of the bar represents a different study site. The same colour bars across the two forest types represent the two adjacent plots of the same site.

A



B



5.3.2. Phenological patterns and climatic variables

The monodominant forest showed statistically significant leaf litter, woody litter, flowering and fruiting variation over time (Fig. 5.7, A–E; Table 5.1). Leaf litterfall and woody litterfall patterns in the monodominant forest were bimodal with two significant peaks (Fig. 5.7, B–C). Flowering and fruiting patterns were all unimodal, having only one significant peak (Fig. 5.7, D–E). The leaf litterfall peaked from late February to early March and in late November (Fig. 5.7B) whereas the woody litterfall peaked in early April and late November (Fig. 5.7C). The flowering peaked in early May and was responsible for the masting of fruit that peaked in September (Fig. 5.7E). The overall phenological patterns in turn accounted for the April, September and November peaks observed for total litterfall in monodominant forest (Fig. 5.7A). However, the variations among the monodominant forest plots during those peak periods were high partly due to the unsynchronized shedding of leaves in *G. dewevrei* among plots (Table 5.1).

The mixed forest had two apparent peaks for total litterfall in late November and from early March to early April (Fig. 5.7A). The leaf litterfall phenological pattern was also bimodal with two peaks in late January and from late February to early April (Fig. 5.7B). Woody litterfall in the mixed forest peaked in early April, late July and late November (Fig. 5.7C). The fruiting seasons in mixed forest were in early October and mid-January (Fig. 5.7E) but these significant peaks were small compared to the monodominant forests. Flowering had no apparent peaks (Fig. 5.7D). Also, the variation among the three mixed forest plots in respect to the phenological patterns of the total litterfall and each litter category was not significant (Table 5.1).

In the monodominant forest, averaged monthly rainfall had no significant relationship with any litterfall variables. Averaged monthly temperature also had no significant relationship with any litterfall variables in the monodominant forest, except for total litterfall, which was negatively correlated with temperature (Table 5.2). Litterfall variables from the mixed forest did not correlate with averaged monthly rainfall or with averaged monthly temperature (Table 5.2).

Figure 5.7 Litterfall patterns of various litter categories in monodominant (red lines) and mixed (blue lines) forests spanning from April 2007 to March 2008: (A) total litterfall mass; (B) leaf litter; (C) woody litter; (D) flowers; and (E) fruits/seeds. The error bars represent 95% confidence intervals ($n = 3$). The amount of litterfall is expressed in $\text{Mg dry mass ha}^{-1}$. Red arrows show the peaks in the monodominant forest and blue arrows indicate the peaks in the mixed forest.

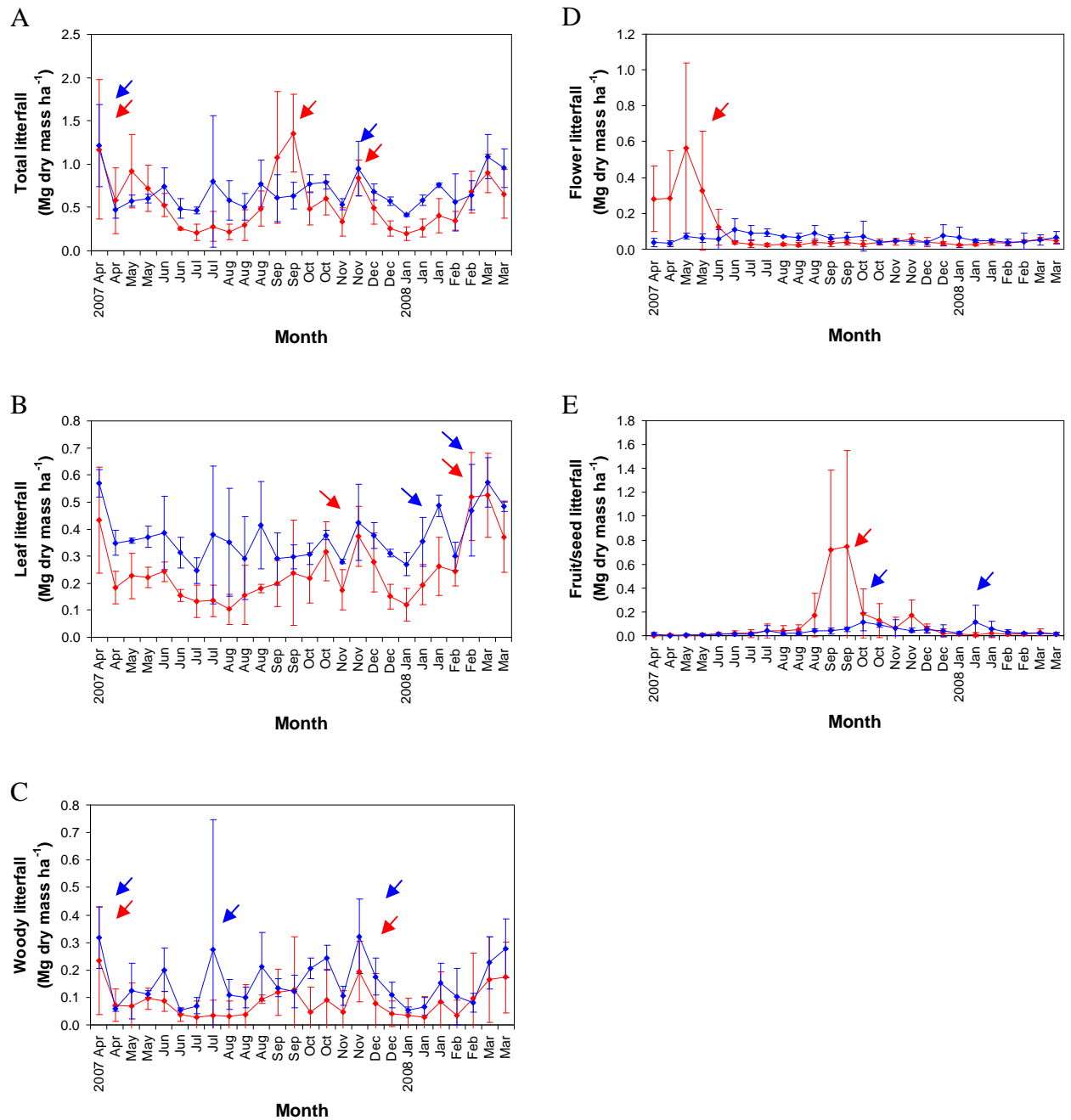


Table 5.1 Statistics for collection date and site effects on total litterfall mass and litter categories. General linear model (GLM) analyses of covariance were performed on data from the monodominant ($n = 30$) and mixed forest quadrats ($n = 30$) separately. Total litterfall mass, leaf litter, woody litter, flowers and fruits/seeds were measured from April 2007 to March 2008. $P < 0.001$ is denoted by ** and $P < 0.05$ by *.

Forest types	Litterfall category	GLM Analyses of Variance					
		Effect of collection date			Effect of plot location		
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>	
Monodominant	Total litterfall	4.91	<0.001	**	4.74	0.013	*
	Leaf litter	6.11	<0.001	**	6.60	0.003	*
	Woody litter	3.45	<0.001	**	3.11	0.054	
	Flowers	4.25	<0.001	**	4.47	0.016	*
	Fruits/seeds	3.72	<0.001	**	6.54	0.003	*
Mixed	Total litterfall	2.73	0.001	*	2.77	0.072	
	Leaf litter	2.85	0.001	*	1.50	0.234	
	Woody litter	1.88	0.029	*	0.49	0.618	
	Flowers	1.27	0.236		0.49	0.616	
	Fruits/seeds	2.08	0.014	*	0.08	0.924	

Table 5.2 Spearman rank correlation coefficients between climatic variables and litter categories in monodominant and mixed forests. The significance was subjected to Bonferroni corrections and was established for P value < 0.005 (denoted by *) because for each climatic variable, there was a multiple significance test of 10 correlation analyses.

Forest types	Litter category	Spearman's Rank Coefficient Tests				
		Mean monthly rainfall		Mean monthly temperature		
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Monodominant	Total litterfall	0.421	0.032	-0.545	0.004	*
	Leaf litter	-0.046	0.823	-0.026	0.898	
	Woody litter	0.217	0.287	-0.337	0.092	
	Flowers	0.256	0.207	-0.301	0.135	
	Fruits/seeds	0.220	0.281	-0.242	0.234	
Mixed	Total litterfall	0.095	0.646	-0.152	0.459	
	Leaf litter	-0.129	0.530	0.103	0.616	
	Woody litter	0.204	0.316	-0.322	0.109	
	Flowers	0.123	0.551	0.004	0.984	
	Fruits/seeds	-0.121	0.555	-0.053	0.796	

5.3.3. Effects of diversity

Temporal variability in community litterfall mass in monodominant forest, measured as the SD of quadrat log-transformed litterfall biomass for one year, was negatively correlated with mean trap species number (Spearman rank coefficient = -0.74, $P < 0.001$), median trap species number (Spearman rank coefficient = -0.69, $P < 0.001$), and modal trap species number (Spearman rank coefficient = -0.62, $P < 0.001$) (Fig. 5.8). There were no patterns in temporal variability and no significant correlations between SD of log-transformed litterfall mass of the monodominant forests and the other three measures of diversity (quadrat species number, Simpson's diversity index and quadrat species evenness; Fig. 5.9, A–C). No measures of diversity were significantly correlated with the SD of log-transformed litter mass in mixed forests (Fig. 5.8, A–C; Fig. 5.9, A–C).

GLM analyses of covariance show that mean trap species number in monodominant forest remains a significant influence on the SD of log-transformed litterfall mass ($F = 4.51$, $P < 0.05$); in models with the SD of log-transformed litterfall mass as the dependent variables, mean trap species number as covariates, and plot location as a random factor. More importantly, the effect of species richness remained significant in GLM analyses of covariance when the potential effects of plot location were accounted for. However, median trap species number ($P = 0.10$) and modal trap species number ($P = 0.17$) failed to remain significant in GLM analyses of covariance.

When data from monodominant and mixed forests were pooled, I observed a significant cubic regression of trap species number (mean: $r^2 = 0.68$, $P < 0.001$; median: $r^2 = 0.66$, $P < 0.001$; mode: $r^2 = 0.62$, $P < 0.001$) against SD of log-transformed litterfall mass (Fig. 5.8). Thus, litterfall mass variability tends to relate to diversity, and the quadrats with higher dominance of *G. dewevrei* (trap species number < 5.0) tend to have higher log litterfall mass SD in the monodominant forest, whereas assemblages with a high number of species in mixed-forest quadrats (trap species number > 5.0) had relatively lower SD when compared with the quadrats in monodominant forest (Fig. 5.8).

Figure 5.8 When data were analysed separately for each forest type, significant correlations were observed for monodominant forest: (A) between standard deviation of log-transformed litterfall mass (SD) and mean trap species number (Spearman rank coefficient = -0.74 , $P < 0.01$); (B) between SD and median trap species number (Spearman rank coefficient = -0.69 , $P < 0.01$) and (C) between SD and modal species number (Spearman rank coefficient = -0.62 , $P < 0.01$). Those from the mixed forest (blue circles; $n = 30$) were all insignificant. When data were pooled from both forest types, the significant cubic regressions indicate the dependence of stability on tree diversity: (A) mean trap species number: $r^2 = 0.68$, $P < 0.001$; (B) median trap species number: $r^2 = 0.66$, $P < 0.01$; (C) modal trap species number: $r^2 = 0.62$, $P < 0.01$).

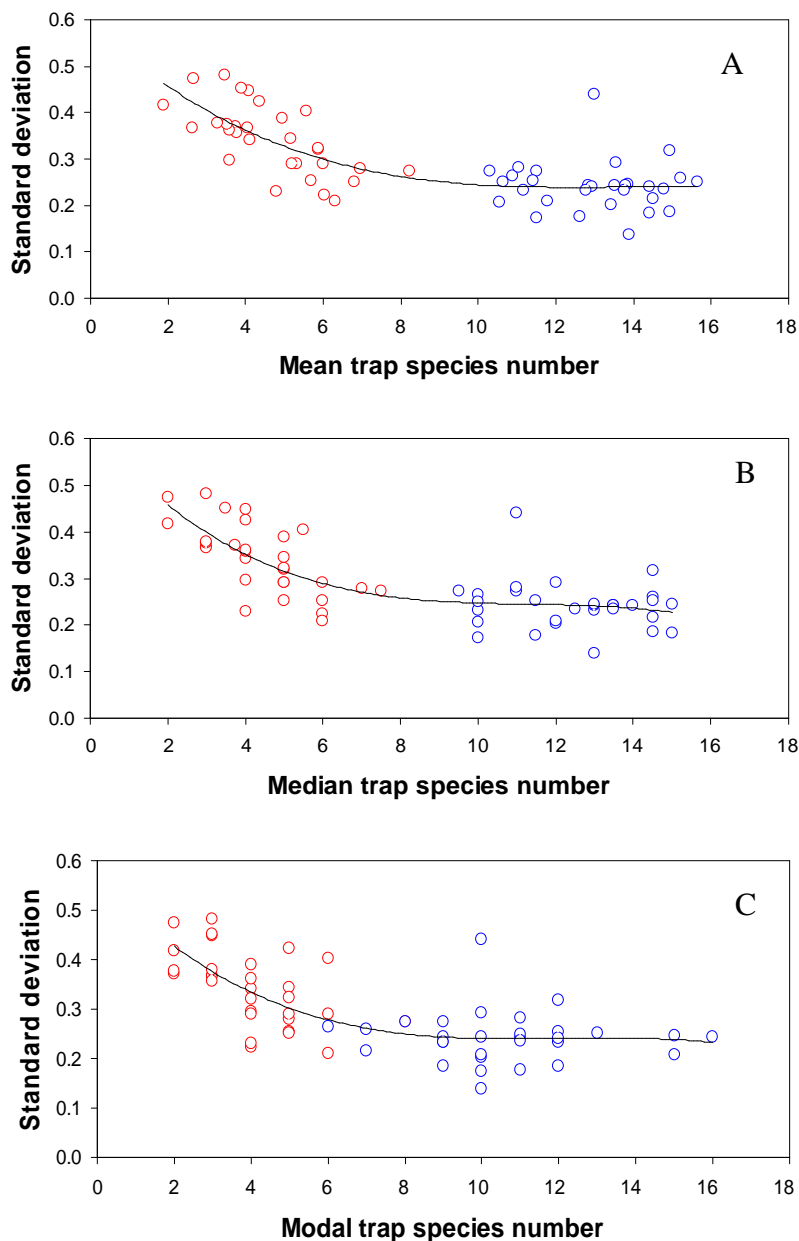
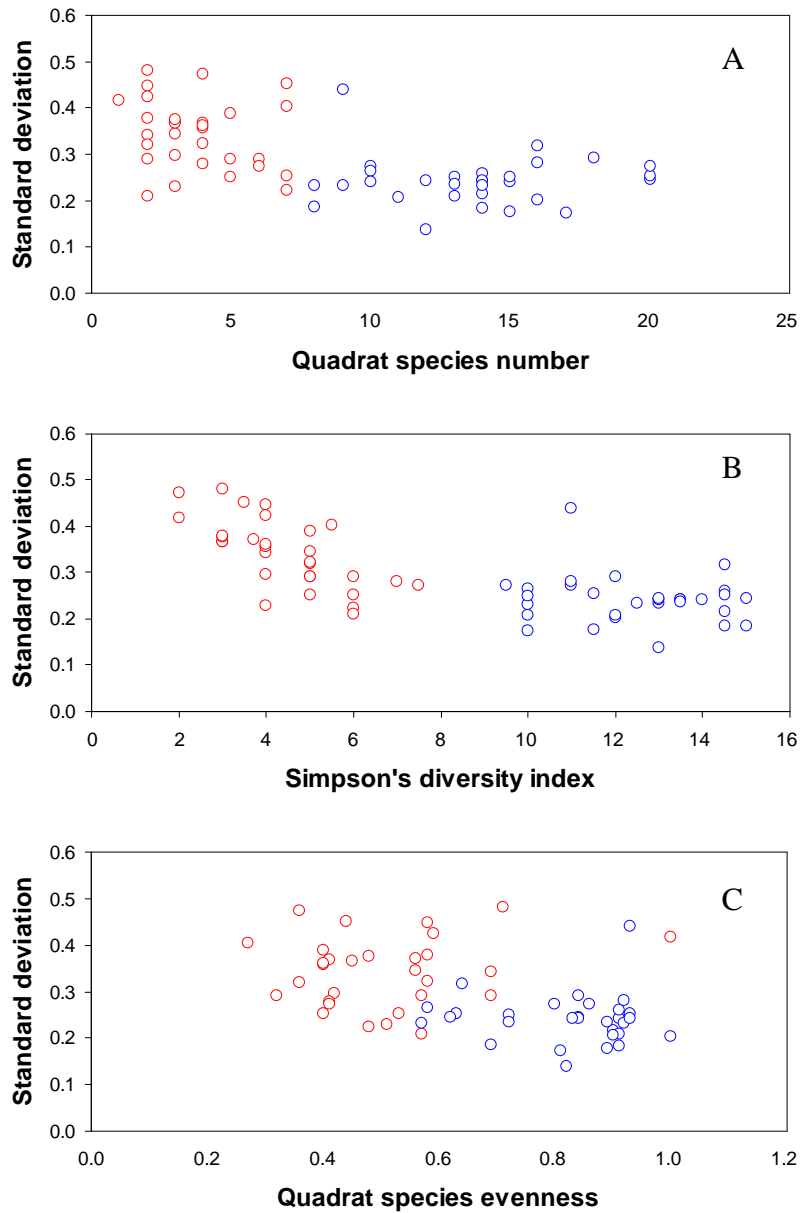


Figure 5.9 The scatterplots from the monodominant forest (red circles; $n = 30$) and mixed forest (blue circles; $n = 30$): (A) between standard deviation of log-transformed litterfall mass (SD) and quadrat species number; (B) between SD and Simpson's diversity index; and (C) between SD and quadrat species evenness. No measures of diversity were significantly correlated with the SD in both forest types.



The 30 focal quadrats in the monodominant forest contained six non-dominant species that had more than three individuals (Table 5.3). Among these six species, the one with the most total number of individuals was *Carapa procera* (nine stems). I retested the diversity-stability relationship using partial correlation to hold the influence of these common species constant. The partial correlations between the mean trap species number and temporal variability of litterfall mass, when the influence of common species was held constant, revealed that the diversity-stability relationship remained highly significant (Table 5.3). Therefore, the change in temporal variability could still be explained by the species diversity when differing species composition was accounted for.

Table 5.3 Partial correlations used to assess whether mean trap species number independently affected the temporal variability of log-transformed litterfall mass in monodominant forest after statistically controlling for effects of species composition. Only six species had three or more individuals found in the 30 quadrats within the monodominant forest. The significance was established for P value <0.008 after Bonferroni correction (denoted by *).

Controlling for	Number	Correlation coefficient	P
<i>Angylocalyx pyaerthii</i>	4	-0.702	<0.001 *
<i>Carapa procera</i>	9	-0.692	<0.001 *
<i>Irvingia gabonensis</i>	3	-0.716	<0.001 *
<i>Mammea africana</i>	4	-0.702	<0.001 *
<i>Strombosia pustulata</i>	3	-0.711	<0.001 *
<i>Trichoscyha acuminata</i>	5	-0.724	<0.001 *

5.4. Discussion

Total litterfall (excluding fine wood [1–10 cm diameter] for comparison with other studies; Clark *et al.* 2001) in monodominant forest (13.47 ± 3.56 Mg dry mass ha^{-1}) and mixed forest (16.37 ± 1.68 Mg dry mass ha^{-1}) was observed to be higher than the estimated values for tropical South American forests (6.70–10.52 Mg dry mass ha^{-1} , Chave *et al.* 2009b), but within the range (1.8–18.6 Mg dry mass ha^{-1}) estimated for other tropical forests (*cf.* Clark *et al.* 2001; Vitousek 1984). Litterfall in both forest types occurred throughout the year and was dominated by leaf-fall (monodominant forest: $45\% \pm 12\%$; mixed forest: $54\% \pm 2\%$). Biomass allocated to the leaves for the monodominant forest (6.36 ± 1.20 Mg dry mass ha^{-1}) was within the range reported for other tropical forests (3.18–8.54 Mg dry mass ha^{-1} , *cf.* Leigh 1999; tropical South American forests: 3.91–7.57 Mg dry mass ha^{-1} , Chave *et al.* 2009b), whereas that of the mixed forest (9.63 ± 0.64 Mg dry mass ha^{-1}) was greater than the higher end of the range. This implies that the mixed forest studied may be one of the more productive tropical forests in terms of leaf production. One of the possible reasons is that the mixed forest in the reserve is constantly being disturbed by the elephants and gorillas. Both foraging elephants and nesting gorillas can create small gaps that in turn, setting more light into the canopy. Such observations are consistent with other high-productivity forests (e.g., Young *et al.* 2009).

My results in the monodominant forest mirror those of Tilman (1996) in finding a negative correlation of temporal variability of litterfall mass with diversity. Communities depauperate in species were more variable whereas greater asynchrony among species in richer communities might lead to a dampening of the variability of the aggregate community litterfall mass. In this study, the lower temporal variability in higher-diversity quadrats may be the result of biological differences in response to seasonal changes in the environment among species in richer communities. For example, quadrats having higher species richness tend to contain a greater number of species with different litterfall phenology patterns. When observed at a community level, all these patterns would generate a relatively more aseasonal pattern and therefore leading to lower variability in litterfall throughout the year. However, the negative

relationship between variability in litterfall mass and species richness was not shown within the mixed forest whereby species richness had no effect on the temporal variability. In fact, my data showed that stabilization of litterfall is already reached by approximately ten species contributing to the litterfall traps (Fig. 5.8).

To explain the difference between the two forest types, it is necessary to examine the magnitude of temporal variability and species richness in the mixed forest. Mixed forests are typically of high-diversity and such vegetation potentially contains many species of different litterfall phenology patterns. Within each community, the overlapping litterfall peaks of different species might cause greater asynchrony in litterfall phenology patterns, and in turn result in temporal variability of relatively low magnitude (standard deviation between 0.2 and 0.3; Fig. 5.8). Therefore, when the environmental conditions change, the relative contributions of each species may change, but not overall litterfall among these highly diverse systems.

My observational study of a natural forest system, containing a gradient of species richness, exhibited similar patterns to those shown by experimental studies (e.g., McGrady-Steed 1997). My results are also comparable with those of long-term grassland experiment (Tilman *et al.*, 2006). These studies have shown that temporal variability of biomass production decreasing nonlinearly with species richness with an asymptote of approximately 10 species. Subsequently, the temporal variability remained unaffected by further increases in diversity. The pattern in my study suggests functional redundancy as inputs to a given point location, among species in communities with higher diversity than 10 species.

Although a one-year study was relatively short, my observations spanned two dry and two wet seasons. Hence, this study sheds some light on the causal relationship between climatic variables and total litterfall. Theory predicts that litterfall increases during the dry season because water stress is linked to a complex physiological process that leads to the death and shedding of vegetative organs, resulting in high litterfall during low water availability in seasonal forests (e.g., Hopkins 1966). During the study period, the dry season spanned from June to August 2007 and from December 2007 to February 2008 (Fig. 5.1). However, the Dja Faunal Reserve is covered in evergreen forest, and perhaps unsurprisingly in my study, the total

litterfall in the monodominant and mixed forests was not affected by the rainfall. While the total litterfall in the mixed forest was not affected by the temperature, that of the monodominant forest actually increased when the temperature was lowered. This suggests that neither of the two dry seasons in the year studied were severe enough to cause a major leaf-fall.

Results from other studies on the effects of climatic variables on litterfall in tropical forests have also proven inconclusive. For example, Songwe *et al.* (1988) have reported that litterfall is negatively correlated with rainfall in Cameroon; whereas Proctor *et al.* (1983) have showed that the environmental factors have no clear effects on the tropical forest litterfall in Borneo. Moreover, Zalamea & González (2008) have claimed that it is the solar radiation rather than other environmental factors that has an effect on the leaf-fall in tropical forest. Thus, I suggest that the association between litterfall and climatic variables remains weak and equivocal.

Also, I suggest that the pattern of litterfall observed in the monodominant forests reflects a species-specific pattern of *Gilbertiodendron dewevrei*. After all, *G. dewevrei* comprised 75 % of all stems found in my 30 focal quadrats. And in this case, the total litterfall of *G. dewevrei* was significantly correlated to average monthly temperature. But the significant effect of plot location (i.e., spatial variability) on litterfall pattern for the monodominant species indicates that the climate is not the only factor triggering litterfall. Intrapopulation genetic variability and microclimatic differences might explain this variation (Zalamea & González 2008).

Finally, temporal variability for most litterfall categories and total litterfall mass was lower in mixed forest plots than in monodominant forest plots. Also at quadrat level within monodominant forest, species richness affected the temporal variability of litterfall biomass. My results show a decrease in temporal variability of community litterfall biomass with an increase in species richness within the monodominant forest. Less litterfall biomass variability indicates that the communities of higher species richness were more stable than communities that were more dominated by *G. dewevrei*.

These observations are encouraging indications of the conservation potential for tree species diversity in tropical agroforestry where predictability of tree production is important. However, at a given point location in the mixed forest, a set of 10 to 16 species can contribute to a single litterfall point; stability in litterfall production actually starts to reach optimal level with about 10 species. Therefore, approximately up to 38 % of species are likely to be redundant. Nevertheless, although the mixed forests may have species with largely redundant functional roles with respect to litterfall stability, their more stable litterfall productivity should allow more animal species to persist in these high-diversity forests. In addition, I emphasize that the maintenance of high biodiversity is still desirable because diversity may differently affect different ecological processes and their variability (Tilman *et al.* 1996).

5.5. Summary

- There were significant differences between the monodominant and mixed forests in the biomass produced for the various litterfall categories whereby the biomass of leaves (absolute value) and woody litter (absolute and proportional values) was higher in the mixed forest; biomass allocation to leaves was not significantly different.
- Three main litterfall peaks were observed in the monodominant forest: April, September and November, significantly correlated to averaged monthly temperature. The mixed forest had only two litterfall peaks in March–April and November, which were associated with neither rainfall nor temperature.
- Increased diversity within the monodominant forest corresponded with decreased temporary variability in litterfall productivity. However, increasing diversity had no effect on the temporal variability of litterfall productivity within the mixed forest where the magnitude of temporal variability was low.
- Species richness independently affected temporal stability of litterfall productivity in the monodominant forest and its effect was not confounded by differing species composition.

6. Effects of tree species diversity on leaf litter decomposition

6.1. Introduction

Litter decomposition is a major pathway for nutrient cycling by which carbon (C), nitrogen (N), phosphorous and other elements move from plants to the soil, back to plants and to the atmosphere (Coûteaux *et al.* 1995). Understanding the influence of different factors, such as physical and chemical properties of plant litter, known as ‘litter quality’ (Aerts 1997), soil fauna (Heneghan *et al.* 1999), and environmental variables (Meentemeyer 1984) on litter decomposition form the basis of many decomposition studies. The main factors that control decomposition rates in different ecosystems in different environments may vary. While litter quality and climate are considered to be the more important determinants in controlling the decomposition rates in temperate ecosystems (Meentemeyer 1984), biotic factors (i.e., the decomposer community) appear to have a greater impact on the regulation of decomposition in tropical ecosystems (Lavelle *et al.* 1993). In tropics, however, contributions of the soil fauna may vary among the vegetation types (e.g., lowland and montane forests; González & Seastadt 2001). Furthermore, the rate and timing of decomposition may vary due to the differing species that produce the litter and therefore contributes to the dynamic cycling of nutrients (Silver & Miya 2001).

The importance of litter diversity in determining decomposition rates has only been assessed in a handful of studies (Hättenschwiler *et al.* 2005), despite knowledge that plant species composition can affect the ecosystem nutrient cycling (Chapman *et al.* 1988). The potential mechanisms of the litter-diversity effects on decomposition include nutrient transfer by fungi among leaf litter from different species, microbial inhibition or stimulation by specific litter compounds, and positive feedback of soil fauna due to improved microenvironmental conditions (see Hättenschwiler *et al.* [2005] for more details). However, most previous studies that considered mixtures of different litter species involved temperate ecosystems, with only one study from a tropical experimental site in Panama (Scherer-Lorenzen *et al.* 2007). Using six

native tree species, with 1-, 3-, and 6-species mixtures in a total of 24 experimental plots, they found “no overall effect of litter diversity if the entire litter mixtures were analysed, i.e. mixing species resulted in pure additive effects and observed decomposition rates were not different from expected rates. However, the individual species changed their decomposition pattern depending on the diversity of the litter mixture, i.e. there were species-specific responses to mixing litter” (Scherer-Lorenzen *et al.* 2007).

A better understanding of the litter-diversity effects on decomposition rates in tropical African monodominant and their adjacent mixed-species forests is of importance for theoretical and applied reasons. First, decomposition in terrestrial ecosystems which mostly comprised mixed-species litters, contributes a significant annual CO₂ flux (approximately 60 Tg C yr⁻¹) to the atmosphere via heterotrophic respiration (Gholz *et al.* 2000). Decomposition studies in tropical African forest systems can thus contribute to the global ecosystem C models (e.g., Gholz *et al.* 2000) which require knowledge on factors influencing decomposition over a broad range of ecosystems, plant functional groups and climates. Second, comparisons of decomposition dynamics between the monodominant and mixed-species tropical forests give a possibility of studying the effects of differing diversity with the same climatic condition *in situ*, which may contribute to our understanding of the natural systems. Last, in the face of rapid loss of biodiversity (Bradshaw *et al.* 2009), it is essential to know how lower plant diversity affects decomposition to better understand how to maintain key processes in tropical ecosystems if plant species richness declines. Furthermore, no previous work has studied the effects of litter mixtures in a tropical lowland forest setting. Also, no previous study has compared the decomposition processes of litter mixtures between the monodominant and mixed forests in the tropics.

The present study is in two parts, first I quantify the amounts of leaf litterfall and ground litter of the monodominant and mixed forest systems to calculate the estimated decomposition rates. Second, I conduct a factorial experiment using leaf litter of two-species mixture (*Gilbertiodendron dewevrei* and *Lauru nobilis*) for comparison of decomposition rates to single-species litters (one of the two component species of the mixed litter). If the

decomposition rates are affected by the litter diversity (i.e., mixture of litters), I expect a change in the decay of each component species in the mixture when compared to the decomposition rates on the basis of single-species.

This litterbag experiment involves two treatments as it was conducted in both low-diversity monodominant forest and high-diversity mixed forest, to examine the effects of litter diversity on decomposition dynamic across the spatial scale of the two forest types. The experiment also involves two levels in which I examine the responses of individual species within the litter mixtures to facilitate comparison between the high-quality litter (*Laurus nobilis*) and low-quality litter species (*Gilbertiodendron dewevrei*) responses where their roles may differ in different forest types. I also consider the role of tree species diversity on decomposition processes and the temporal pattern of the mixed-litter effects to demonstrate the complexity of decomposition processes in the tropics.

I addressed the following questions: (1) What is the proportion of litter produced by *Gilbertiodendron* sp. on the forest floor of the monodominant *Gilbertiodendron dewevrei* forest and does the *Gilbertiodendron* leaf litterfall abundance correlate with tree species diversity within the monodominant forest? (2) Does tree species diversity affect estimated decomposition rates observed in the two forest types and those derived from the litterbag experiments? (3) Do the two litter species of contrasting initial quality affect each other's decomposition rates when they are mixed? (4) Does each of these litters of different quality and their mixtures show similar patterns of variation over time in the two forest types?

6.2. Methods

Three independent patches of monodominant forest and their corresponding adjacent mixed forest in the Dja Faunal Reserve were used for this work between April 2007 and March 2008 (for details of study sites, see Chapter 2). At each site, one 1 ha plot (100m ×100 m) of monodominant forest and another plot of the same size in the adjacent mixed-species forest were established (for details on plot establishment, see Chapter 2). In total, I had six plots

consisting of three pairs of monodominant and mixed-species forest plots. Each plot was divided into 25 quadrats (20m × 20m) and all tree stems ≥ 10 cm in diameter at breast height (dbh) in all quadrats were identified. For each quadrat, I calculated the Simpson's tree diversity index (for tree measurement protocol, see Chapter 3).

6.2.1. Litterfall observations

I collected leaf litterfall by placing three litterfall traps (0.5m × 0.5m, 1 mm mesh) in each of 10 randomly selected quadrats in each of six plots. The traps were randomly placed at least 5 m away from the perimeter of the quadrats to minimize the influence of the adjacent quadrats (i.e., edge effect) (Wardle & Zackrisson 2005). Fortnightly, I collected the contents of the traps for a period of one year. The amount of *Gilbertiodendron* leaf litterfall derived from the traps in the monodominant forests was used to determine if leaf litterfall abundance of *Gilbertiodendron* sp. negatively correlated with tree species diversity at a small-scale level within the monodominant forest.

Among the quadrats that had litterfall traps, I chose randomly three quadrats from each plot. For each selected quadrat, I calculated the average of the annual leaf litterfall dry mass of the three traps and I measured leaf standing crop dry mass by collecting all leaf litter in an area of equal dimension of a litter trap (i.e., 0.5 m × 0.5 m). The leaf standing crop mass was obtained four times in April 2007, July 2007, September 2007 and January 2008. Subsequently, an average was calculated from the four readings. Decomposition rates for the two forest types were estimated as the dry mass of leaf litterfall ($\text{Mg ha}^{-1} \text{yr}^{-1}$) divided by the dry mass of leaf standing crop on the forest ground ($\text{Mg ha}^{-1} \text{yr}^{-1}$), *sensu* Schlesinger (1991). In total, decomposition rates for 18 quadrats (nine quadrats in each forest type) were calculated and then correlated with their respective tree diversity index.

I analysed the diversity–decomposition correlation by choosing from the different plots: the quadrat with the highest tree species diversity index from all three plots, the quadrat with the lowest diversity index from the remaining two plots and another quadrat with an intermediate

diversity index from the remaining last plot for each forest type. Therefore I had a diversity gradient of a sample size of six pooled together from the two forest types, with each sample deriving from a different plot, to avoid possible pseudoreplication. To further explore the diversity–decomposition relationship, I also reanalysed (1) using all the 18 quadrats from both forest types and (2) each forest type separately.

6.2.2. Litterbag experiments

I compared the decomposition rates of the litter mixtures of air-dried organic bay (*Laurus nobilis*) and newly senescent *Gilbertiodendron dewevrei* leaves (hereafter *Gilbertiodendron* leaves) with those of the single-species litters of respective species in both monodominant forest and mixed forest by using litter bags. I placed five bay-litter bags, five *Gilbertiodendron*-litter bags and five mixed-litter bags in each of 10 randomly selected quadrats in each of six plots at the beginning of the wet season in April 2008. All litter bags were placed randomly in the middle of the quadrats and were pinned to the ground in contact with soil surface. I retrieved one ‘set’ of litter bags (one bay-, one *Gilbertiodendron*- and one mixed-litter bag; randomly chosen) from each quadrat after one, three, five, seven and nine months. After collection, all sample contents were oven-dried (55 °C) to constant weight ($\pm 0.01\text{g}$). Decomposition was calculated as the percentage of initial litter mass lost. To determine the individual species responses to the litter mixtures, mixed samples were separated into species and reweighed. In total, the data set is based on 60 quadrats consisting of 30 monodominant and 30 mixed-species forest quadrats, five collection periods, and a total of 900 litterbags (300 of each bay-, *Gilbertiodendron*-, mixed-species bags).

The litterbag (10cm \times 15cm, 2mm mesh) was made of nylon netting sewn with polyester thread filled with 4.0 g of leaf litter, or 2.0 g of each species in the mixed bags. Another batch of litter bags of standard substrates (bay leaves, $n = 15$; *Gilbertiodendron* leaves, $n = 15$) was oven-dried (55 °C) and weighed to develop the conversion factors that express initial weights of leaf samples in the litter bags as oven-dry mass. I used bay leaves and

Gilbertiodendron leaves as the standard substrates for three practical reasons. First, bay leaves are easily available and are a common standard substrate being used in major pan-tropical study (Jennifer Powers, pers. comm.) and *Gilbertiodendron* leaves are easy to obtain because *Gilbertiodendron dewevrei* dominates the monodominant forests of the study sites. Second, these two substrates varied on initial litter quality. *Gilbertiodendron* leaves—representing the relatively lower quality standard—are thick with high crude fibre (cellulose and lignin) concentration of 63.5 % (Gross *et al.* 2000), whereas the bay leaves are the higher quality standard with a relatively lower crude fibre concentration of 46.8 % (Kutbay 2000). Last, both substrates differed considerably in their colours, texture and characteristics of epidermis and leaf veins, and therefore allowed each species in the mixed-species litter to be accurately separated and weighed.

For each quadrat, I calculated the decomposition rates, k , of the two substrate species in single-species and mixed bags by fitting an exponential decay model to the changes of remaining leaf mass over time:

$$X = 100e^{-kt}$$

where X is the proportion of initial leaf mass remaining at time t (in months); and k is the exponential decay coefficient (Wieder & Wright 1995). This model is considered to be biologically meaningful because it corresponds to our current understanding of the litter breakdown process, with initially rapid decay due to the leaching of water-soluble and easily degraded compounds and slower loss of the remaining more recalcitrant materials over time (Jenny *et al.* 1949; Rubinstein & Vasconcelos 2005). Subsequently, I compared k -values of the substrates in different treatments and forest types using their 95% confidence intervals. I also compared the predicted decomposition rate of the mixed litter (i.e., the arithmetic mean of the two component species) with the observed decomposition rate of the mixed litter as a whole. Finally, I correlated k -values with the tree diversity index (1) for each forest type and (2) using pooled data across the two forest types, to determine if there is diversity effect observed on the two substrate species.

One potential bias in a litterbag experiment is that soil particles, extraneous debris and roots may enter into the bag and affect the accuracy of measurement of mass loss. Therefore, I washed the litters in water, and then removed all sample content with fine tweezers into labelled envelopes before drying. Thus, any problems associated with soil contamination of the processed litters were minimized.

I assessed whether my data was normally distributed using the Kolmogorov-Smirnov test and in cases of multiple comparisons, I applied the Bonferroni correction (Rice 1989). However, the normality of the tree diversity index pooled from the two forest types for my litterbag experiments ($n = 60$) did not improve after data transformation. Therefore, I used non-parametric Spearman rank test for all correlation tests that involved tree diversity index. All statistical tests were conducted using SPSS 13.0 statistical software.

6.3. Results

6.3.1. Observations in two forest types

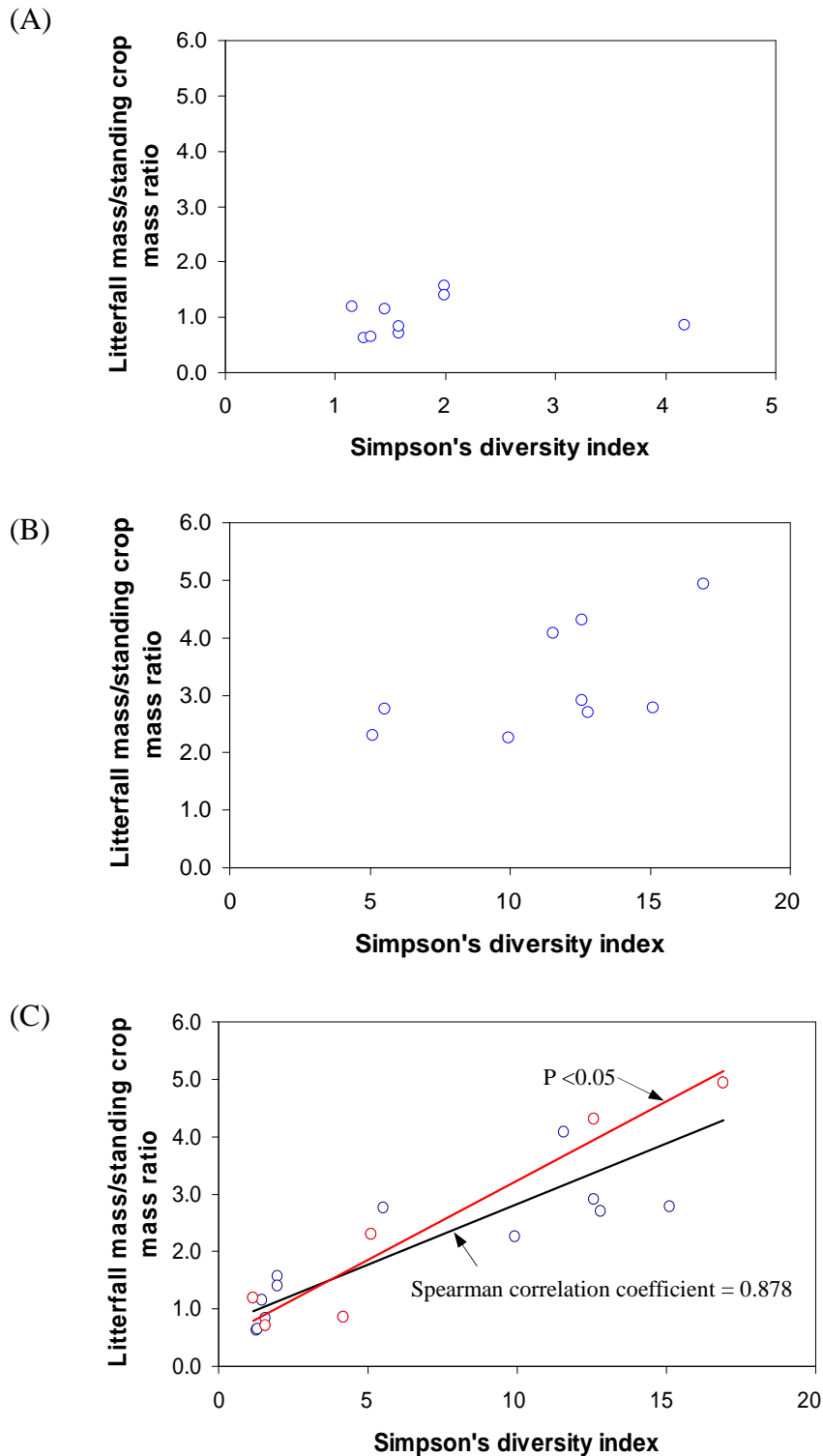
The average leaf-only litterfall dry mass collected was 2.52 Mg ha⁻¹, 2.42 Mg ha⁻¹ and 1.69 Mg ha⁻¹ for the three plots in monodominant forest ($n = 3$ quadrats). The average leaf litterfall mass collected for the three plots of mixed forest was 3.49 Mg dry mass ha⁻¹, 4.08 Mg dry mass ha⁻¹ and 3.20 Mg dry mass ha⁻¹ ($n = 3$ quadrats). The values were obtained by averaging the three quadrats of each plot to avoid pseudo-replication. On average, the monodominant forest produced 2.21 ± 0.42 Mg dry mass ha⁻¹ of leaf-only litterfall annually ($n = 3$ plots) whereas the mixed forest had 3.49 ± 0.47 Mg dry mass ha⁻¹ ($n = 3$ plots). The monodominant forest produced a significantly lower amount of leaf-only litter than the mixed forest, and these results are in consistent with the findings based on 10 quadrats per plot (see Chapter 5). The mean of paired differences in leaf-only litterfall mass between the two forest types was 1.27 ± 0.50 Mg dry mass ha⁻¹. The estimations of leaf-only litterfall dry mass based on only 3 quadrats per plot were relatively lower than those based on 10 quadrats per plot for both forest types (see Chapter

5; monodominant forest: 6.36 ± 1.20 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$; mixed forest: 9.63 ± 0.64 Mg dry mass $\text{ha}^{-1} \text{yr}^{-1}$).

For the average amount of litter standing crop from the four collections throughout the year, the three plots in monodominant forest had 2.02 Mg dry mass ha^{-1} , 2.67 Mg dry mass ha^{-1} and 2.36 Mg dry mass ha^{-1} ($n = 3$ quadrats), and those of the mixed forest had 1.07 Mg dry mass ha^{-1} , 1.27 Mg ha^{-1} and 0.94 Mg dry mass ha^{-1} ($n = 3$ quadrats). On average, the monodominant forest had a significantly greater litter standing crop mass (2.35 ± 0.37 Mg dry mass ha^{-1}) as compared to the mixed forest (1.09 ± 0.19 Mg dry mass ha^{-1}). The mean of paired differences between the two forest types was 1.26 ± 0.30 Mg dry mass ha^{-1} . In addition, the average estimated decomposition rate, using litterfall/standing crop ratio, in mixed forest (3.22 ± 0.63) is significantly higher than that in the monodominant forest (1.00 ± 0.22). The mean of paired differences between the two forest types was 2.23 ± 0.66 .

Simpson's tree diversity index of the six quadrats from monodominant forests ranged from 1.15 to 4.17, whereas those of mixed forests ranged from 5.12 to 16.89. Leaf litterfall/standing crop ratio was not significantly correlated with Simpson's tree diversity when each forest type was analysed separately (Fig. 6.1, A & B). To further investigate the diversity effects, a gradient of Simpson's diversity index between 1.15 and 16.89 was obtained from six quadrats, with one from each of six plots (see Methods). Along this diversity gradient, tree species diversity and the estimated decomposition rates were significantly correlated (Spearman's rank coefficient = 0.83, $P < 0.05$). When I pooled all 18 quadrats, the positive relationship of tree diversity and leaf litterfall/standing crop ratio remained significant (Spearman's rank coefficient = 0.88, $P < 0.001$; Fig 6.1C). The proportions of the total annual leaf litterfall in the three monodominant forests that belong to *G. dewevrei*, were 52%, 75% and 92%, respectively (average proportion: $73 \pm 23\%$). The abundance of *Gilbertiodendron* leaves as a proportion of total litterfall negatively correlated with the tree species diversity at a small spatial scale level (Spearman rank coefficient = -0.35, $P < 0.05$, one-tailed).

Figure 6.1 Leaf litterfall/standing crop ratio is not significantly correlated with Simpson's tree diversity index ($P > 0.05$) when data was analysed separately for the (A) monodominant *Gilbertiodendron* forest, and (B) mixed forest using non-parametric Spearman's rank correlation test. (C) To remove potential pseudo-replication effect, I non-randomly chose a sample size of six quadrats pooled together from the two forest types to represent a wide range of diversity index, with each quadrat deriving from a different plot (red dots) and the trendline (red line) is positively significant. Reanalysis of pooled 18 quadrats from both forest types (black line) remained positively significant.



6.3.2. Mixed-litter decomposition experiments

To assure that the decomposition patterns of the bay leaves, *Gilbertiodendron* leaves and their mixtures in both forest types could be described adequately by the exponential model, I fitted the model to the data collected over 9 months and found that the model fitted the data of the two species in various treatments well ($R^2 \geq 0.8$).

The higher quality bay leaves had higher decomposition rates than the *Gilbertiodendron* leaves throughout the experiment, regardless of being in single-species or mixed-species bags, or being in monodominant or mixed forest (Fig. 6.2, A & B). Overall, being left in monodominant forest for nine months, 73 % and 34 % mass losses were observed for bay leaves and *Gilbertiodendron* leaves, respectively, by averaging over replicates. Over the same experimental period in mixed forest, decomposition of 77 % mass loss for bay leaves and 31 % mass loss for *Gilbertiodendron* leaves were observed. Consistent with percentage litter loss analyses (Fig.6.2, A & B), decomposition k-values for bay litter did not significantly differ between monodominant and mixed forests (Table 6.1). For *Gilbertiodendron* litter, decomposition k-values did not differ when I compared treatments or forest types (Table 6.1). However, the decomposition k-value of bay leaves in mixed-litterbag in the mixed forest was significantly higher as compared to the same treatment in the monodominant forest (Table 6.1). Decomposition k-values of each litter species were not correlated with the tree species diversity index, in single species or mixed litterbags in either forest types, or when data was pooled across forest types (Fig. 6.3, A–D).

The forest type had no impact on the decomposition of the two litter types. Both high-quality bay leaves and low-quality *Gilbertiodendron* leaves experienced a rapid early decay during the first five months and after then the decomposition rates drastically reduced in both forest types (Fig. 6.2, A & B). For each species, there was no difference in decomposition between the two forest types throughout the experimental period (Fig. 6.2, A & B).

Figure 6.2 Litter mass loss (%) of bay (A) and *Gilbertiodendron* leaves (B) in monodominant forest (mono) and mixed forest (mix) over nine months. Single-species treatment is denoted as pure leaves and mixed-litter treatment is mixed leaves. Litter mass loss (C) was also measured in litter mixtures as a whole (mixture) compared with the average of both the bay and *Gilbertiodendron* litter individual losses (predicted value). The bars shows the 95% confidence intervals at $P = 0.05$.

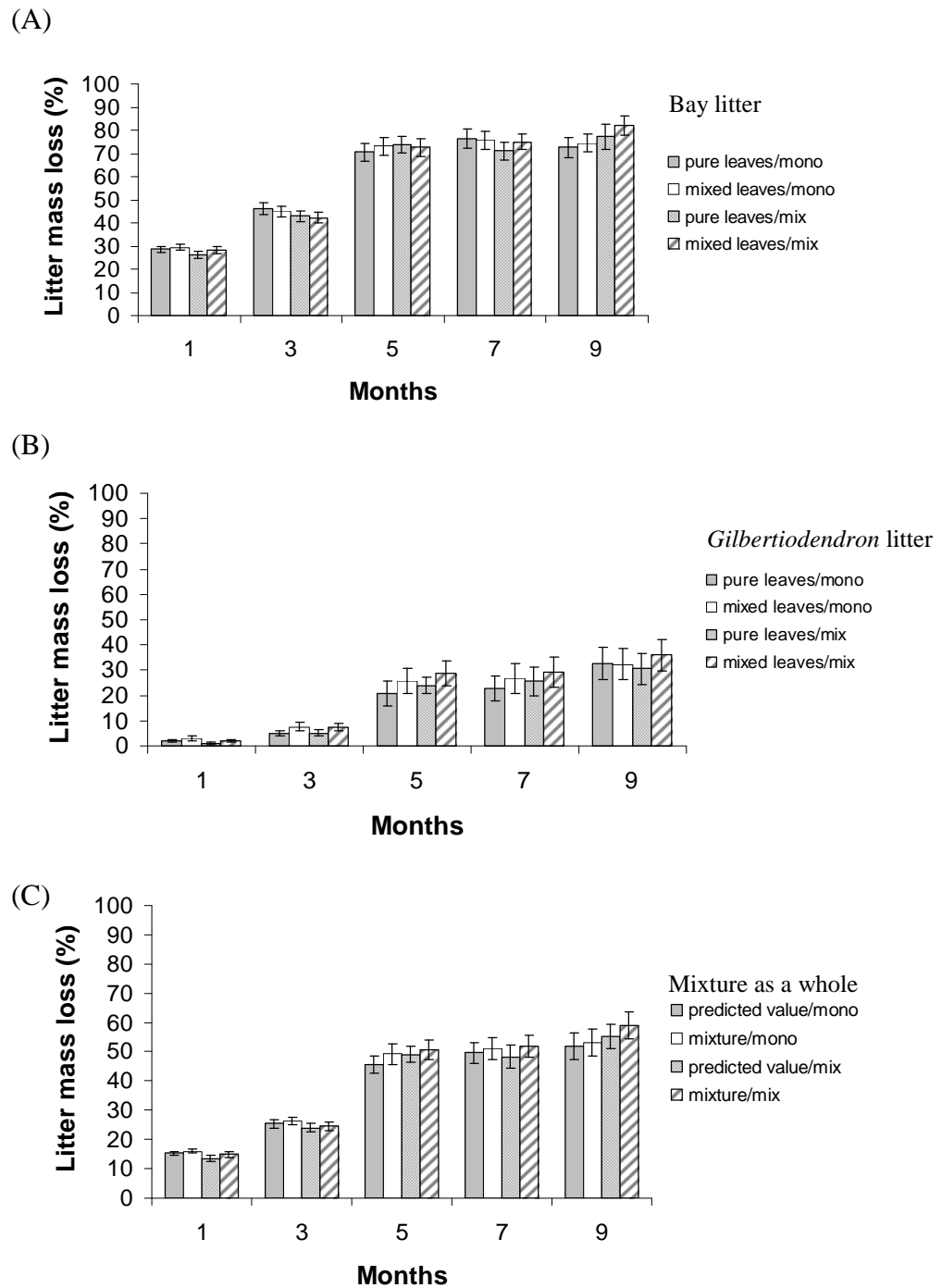
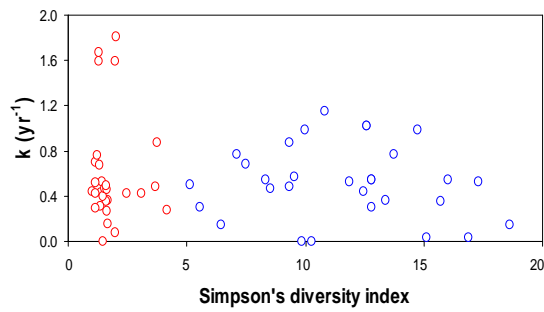


Table 6.1 The decomposition rates (k) of bay and *Gilbertiodendron* litter in both the single-species litterbags and mixed litterbags observed in the monodominant and mixed forest. CI is the 95% confidence intervals at $P = 0.05$.

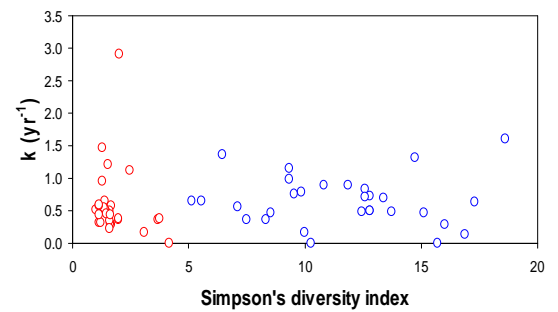
Litter type	Forest type	Treatment	k (yr ⁻¹)	CI
Bay	monodominant	pure	1.9	1.6 – 2.2
		mixed	2.0	1.7 – 2.2
	mixed	pure	2.2	1.9 – 2.5
		mixed	2.6	2.2 – 3.1
<i>Gilbertiodendron</i>	monodominant	pure	0.6	0.4 – 0.8
		mixed	0.6	0.4 – 0.8
	mixed	pure	0.5	0.4 – 0.6
		mixed	0.6	0.5 – 0.8

Figure 6.3 Scatter-plots of decomposition k-values of *Gilbertiodendron* leaves in single-species litterbags (A), *Gilbertiodendron* leaves in mixed-litterbags (B), bay leaves in single-species litterbags (C) and bay leaves in mixed litterbags (D) along Simpson's diversity index in monodominant *Gilbertiodendron* forest (red circles) and mixed forest (blue circles). Decomposition k-values of each species were not correlated with diversity index, in single species or mixed litterbags in either forest types, or pooled data across forest types.

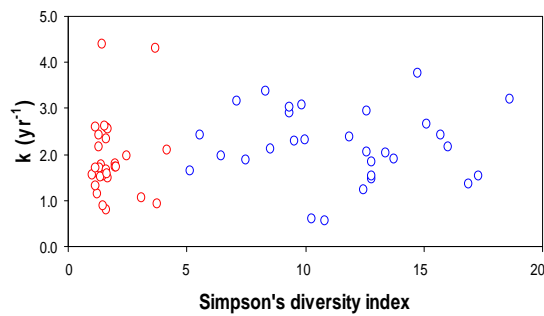
(A) Pure *Gilbertiodendron* leaves



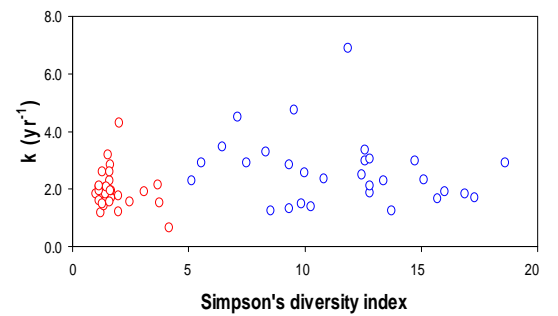
(B) Mixed *Gilbertiodendron* leaves



(C) Pure bay leaves



(D) Mixed bay leaves



The decomposition of the mixed litter as a whole did not differ significantly when the arithmetic mean of component species (i.e., predicted decomposition rate) were compared within forest types and across forest types throughout the duration of the experiment (Fig. 6.2C). After nine months, the predicted litter losses of the mixed litter in monodominant and mixed forests were $51.9 \pm 4.5 \%$ and $55.2 \pm 4.2 \%$, respectively. These values were not significantly different from those observed in mixed litter as a whole in monodominant ($53.3 \pm 4.6 \%$) and mixed forests ($59.0 \pm 4.4 \%$; Fig. 6.2C).

Comparing decomposition patterns between single-species bags and their corresponding species from the mixed bags did not differ except on one accounts: the *Gilbertiodendron* leaves from the mixed bags in the monodominant forest collected after 3 months decomposed significantly faster than those in the single-species bags. Interestingly, the mixed-litter effect was not detectable in the mixed litter as a whole but it was observed only when the individual species was being examined. However, this significant positive litter-diversity effect was not observed during the subsequent collections although in nine out of 10 pair-wise comparisons, regardless of forest type showed that the decomposition rate of *Gilbertiodendron* in the mixed bag was greater than when it was alone in a bag (Fig. 6.2B).

6.4. Discussion

6.4.1. Observational evidence on diversity impacts on decomposition

The mixed forest had a greater mass of leaf litterfall than the monodominant forest, whereas the latter had a greater standing crop mass than the former. This is in agreement with previous observations in similar forest types in the Democratic Republic of the Congo (Torti *et al.* 2001). This implies that in general, the mixed forest had greater leaf production and faster decomposition of resulting leaf litter than the monodominant forest. On average, the mixed forest produced 58% more leaf litterfall and its leaf litter decomposed three times faster than their monodominant counterpart. This is despite the apparently indistinguishable soil properties, topography and climate of the two forest types in the Democratic Republic of the Congo (Hart

1985, Hart *et al.* 1989, Conway 1992) and the plots studied here (see Chapter 2). This shows the potential impacts of individual species and diversity on productivity and decomposition. In the monodominant forests, a large proportion of the leaf litterfall is produced from the monodominant species. This, together with the slow decomposition of their leaves, has been hypothesized as one of the traits that the monodominant species use to modify the understorey environment so as to prevent the establishment of other species there (Torti *et al.* 2001).

I examined the effects of plant diversity on the estimated decomposition rates derived from the litterfall/standing crop ratio. Viewed alternatively, I examined the leaf litter breakdown over a range of differing environments provided by tree communities of differing diversity among my quadrats. I found that tree diversity was positively correlated with decomposition. However, the direction of the correlation disagrees with the previous observations from temperate forests that higher tree species number tended to slow down leaf litter decomposition (Madritch & Cardinale 2007). Also, the tree diversity-decomposition relationship is not significant if I analysed the data separately for each forest type using non-parametric Spearman's rank correlation test (Fig. 6.2), indicating the diversity effect is weakened when the data from one of the forest types is ignored. This suggests two implications: first, an average of 73% of the total annual leaf litterfall in the monodominant forests belonged to *Gilbertiodendron* explicitly illustrates that the natural dominance of a single species appears to be the mechanism responsible for decreasing decomposition rates whereby only one species contributed a large proportion of low-quality litters at a small spatial scale level. This could be an example whereby dominance by tree species with inherently lower litter quality could underlie the positive relationship between species diversity and leaf litter decomposition rate. Second, the tree diversity effect, may depend on the range of the species diversity gradient studied and may only be detectable if the diversity range is sufficiently wide and sample sizes are sufficiently large. Thus, I cannot rule out the possibility that the lack of strong correlation between diversity and decomposition rate within each forest type was due to the small sample sizes.

It has been suggested that decomposition rates may be influenced by an interaction of many variables, such as soil fauna (Heneghan *et al.* 1999) and environmental conditions

(Meentemeyer 1984). However, I did not conduct surveys on the decomposer communities and the environmental parameters, such as temperature and pH, in my quadrats when the experiments were carried out. Since I do not have data on the many local biotic and abiotic variables, it is difficult to pin point the variables affecting decomposition. Further research will be required. Nevertheless, across both forest types, my results show that there is strong correlation between tree diversity and litter decay rate, and thus this may imply that the potential influences of soil organisms and the abiotic conditions coupled to tree species richness on litter decomposition may be substantial.

6.4.2. Experimental evidence on effects of litter mixture

My observed bay and *Gilbertiodendron* litter decomposition rates, expressed as exponential decay k-values, are 1.9–2.6 yr⁻¹ and 0.5–0.6 yr⁻¹, respectively. The decomposition rates of bay litter were in the range as compared to the typical rate of >1.0 yr⁻¹ of tropical forests (Didham 1998; Scherer-Lorenzen *et al.*, 2007) whereas those of the *Gilbertiodendron* litters were comparatively lower. However, the decomposition rates of *Gilbertiodendron* leaves were comparable to those of 0.6–0.7 yr⁻¹ of another monodominant species, *Peltogyne gracilipes*, in Neotropics (Villela & Proctor, 2002).

My experiment comparing the decomposition of the single-species bags between the forest types and between two-litter species suggests three patterns: First, the decomposition rates for each species were the same across the two forest types. However, the similarity in the decomposition rates does not necessarily mean that these forest types shared the same biotic conditions. For example, Torti *et al.* (2001) noted lower numbers of leaf litter arthropods in African monodominant forest compared to the mixed forest, even though there was considerable overlap among the orders represented between the two forest types. One possible explanation for the same decay rates across different forest types is the exclusion of macroarthropods in my study. I recognized that the small mesh size of the litter bags may exclude the larger soil invertebrates such as earthworm, millipedes and snails that have potential of processing larger

amount of leaf litter. Though I did find microarthropods in the litterbags, the lack of macrofauna may lead to a failure to detect differences in decomposition rates between the two forest types if their macrofauna differs. Nevertheless, the similar k-value across the two forest types does reflect that the abiotic environment was similar among the forest sites.

My findings that show each standard litter species had the same decomposition rate between the two forest types appear to contradict my direct observations that litter in the mixed forest decomposed three times faster than that in the monodominant forest. Using standard litter species is probably not a good surrogate for measuring the overall decomposition rates in these forests. But, this study was designed with an aim to investigate if decomposition rate of monodominant forest (K_{mono}) and that of mixed forest (K_{mix}) are different, given standard species of different initial litter quality. However, a new calculation of $K_{\text{mix}}/K_{\text{mono}}$ ratio based on the litterbag experiment data (Table 6.1) with the knowledge of the average proportion of *Gilbertiodendron* leaves on the monodominant forest floor (i.e., 0.73), shows that the difference in decomposition rates between the two forest types was about three-fold. The new calculation of $K_{\text{mix}}/K_{\text{mono}}$ ratio is:

$$\begin{aligned} K_{\text{mix}}/K_{\text{mono}} \text{ ratio} &= K_{\text{mix}} / (P_g \times K_{\text{gm}}) + (P_{\text{ng}} \times K_{\text{bm}}) \\ &= 2.63 / (0.73 \times 0.60) + (0.27 \times 1.96) \\ &= 2.7 \end{aligned}$$

where K_{mix} is the average decay rate of the bay leaves in the mixed bags in mixed forests; P_g and P_{ng} are the average proportions of *Gilbertiodendron* and non-*Gilbertiodendron* leaves on the monodominant forest floor, respectively; K_{gm} is the average decay rate of the *Gilbertiodendron* leaves in the mixed bags in monodominant forests; and K_{bm} is the average decay rate of the bay leaves in the mixed bags in monodominant forests. Thus, the discrepancy between the estimated decomposition rates from direct observation and those from litterbag experiment can be reconciled. The three-fold difference observed may be due to the dominance of *G. dewevrei*.

The second distinct pattern is that the rates of decomposition for the two standard litter types in both forest types decreased drastically after five months. The litterbag experiment started in the beginning of the wet season, thus rain likely facilitated the leaching of the water-

soluble compounds and washed away the easily degraded compounds in the litter. The remaining litters after five months, which coincided with the wettest month of the year, were the recalcitrant part of the leaves. However, the exclusion of macrofauna in my study might also have slowed down the loss of the recalcitrant materials after five months.

Third, my results confirmed the findings from previous studies that species of high litter quality have higher decomposition rates than those of low litter quality (e.g., Hättenschwiler *et al.* 2005; Heal *et al.* 1997; Hector *et al.* 2000). High-quality litter may influence the decomposition of the low-quality litter (Hättenschwiler & Gasser 2005). Despite that, my litter mixture experiments show that the low quality litter does not necessarily have faster breakdown when mixed with high-quality litter over a longer temporal scale. The *Gilbertiodendron* leaves of the litter mixtures in monodominant forests collected after three months exhibited positive, non-additive effects of litter-mixing on the decomposition. But this mixing-effect was short-lived and was not observed in the litter mixtures collected after 5 months. In both forest types, litter mixtures of the two plant species that were left for 9 months have no effect on the decomposition of each individual component species. This confirms that the duration of decomposition experiments is a crucial component of their interpretation. Therefore, results from the experiments that examined only short-term decomposition must be interpreted with caution.

The interplay between the forest type (i.e., mixed forest) and the litter composition (i.e., mixed litter) may enhance the breakdown of a particular litter type (i.e., high-quality litter). This is highlighted when I compared the decomposition rates of bay litter in the mixed forest–mixed litter combination with the bay litter (of both single species and mixed bags) in the monodominant forest. This implies that diversity effects on decomposition may only manifest along a wider range of plant diversity index. Also, it is broadly consistent with one study using temperate species that found positive effect on litter nutrient release when litter composition and microenvironment (induced by the plant diversity) were known to interact (Blair *et al.* 1990). Nevertheless, the magnitude of such influence found in my study was small. Tree diversity effects were not detected in my litterbag experiment. This may be due to the inaccessibility of my

experimental litter to the larger soil decomposers which are known to alter leaf litter diversity effects on decomposition (Hättenschwiler and Gasser 2005), or may reflect a lack of litter diversity impacts on litter decomposition.

6.4.3. Limitations

I used equal proportions of two species of litter in the mixed bags. An alternative methodology would be to use species in the proportions in which they occurred in the forests (Hector *et al.* 2000). Although the litter decay is affected by the quality and quantity of litter from different species (Chapman *et al.* 1988), the approach of Hector *et al.* (2000) is not possible in the setting of a tropical forest where litter species composition is (a) difficult to assess accurately and (b) difficult to assemble for placement into 600 litterbags. Actual proportions of species present vary among forest types and within forest types over short distances. Also, my objectives were to investigate the effect of mixing litter of different quality on decomposition. However, since my study on high-quality litter is based on bay leaves, I cannot conclude whether it correctly reflects the decomposition rates of the non-dominant forest species in the monodominant forest and those of the species found in the mixed forest. Similarly, I am not sure if the *Gilbertiodendron* leaves can represent the more recalcitrant litter species in the mixed forest. Thus my study can only provide an estimate of the relative decomposition rates of high-quality and low-quality litters in both forest types.

I used only two species for my litter-mixture decomposition experiments and compared this with the expected value on the basis of single-species decomposition. This limits a thorough assessment of the litter composition effects and restricts a general description of leaf litter decomposition as a function of litter diversity (Hättenschwiler *et al.* 2005). Nevertheless, this study may be the first litter-mixture experiment being conducted in a tropical lowland forest. Also, my standard litter species enables my results to be directly comparable between the two forest types within the study area and other forthcoming comparative studies (Jennifer Powers, pers. comm.). Furthermore, my inclusion of low species number in the experiment enables the

separation of decomposition rates among the species within mixtures. This approach is important because the mass loss measured in litter mixture may mask species-specific responses, as shown in my experiments (Fig. 6.2).

6.5. Summary

- Leaf litterfall production was significantly higher in the mixed forests. However, the amount of litter standing crop was greater in the monodominant forests.
- Estimated decomposition rate (litterfall/standing crop ratio) in the mixed forest was three times faster than that of the monodominant forest.
- Estimated decomposition rates (litterfall/standing crop ratio) were correlated to local quadrat-scale tree species diversity.
- Using litterbag experiment, the decomposition of high quality leaves (*Laura nobilis*) were faster than that of the *Gilbertiodendron* leaves (2.0 yr^{-1} versus 0.6 yr^{-1}) and the decay rates for each of the standard species were the same in both forest types.
- *Gilbertiodendron* leaves decomposed faster when mixed with the higher quality bay leaves between one and three months into the experiment. But this positive mixing-effect was short-lived and was not observed after five and nine months.

7. Conclusion

7.1. Research synthesis

The research presented in this thesis demonstrates the complexity of the relationship between diversity and function in tropical forests. These results could improve our understanding of the effects of tree species diversity on critical ecosystem functions, such as above-ground biomass (AGB) growth, litterfall productivity, above-ground net primary productivity (ANPP), temporal variability of litterfall biomass and leaf litter decomposition.

Table 7.1 provides a summary of the effects of tree species diversity on the ecosystem functions considered in this study. This work used a dataset collected over 2005 to 2008 from six 1 ha plots in the Dja Faunal Reserve, where mature forests of lower- and higher-diversity naturally co-exist. For each forest type, three 1 ha plots were further divided into 20 m × 20 m quadrats where field measurement of AGB growth accompanying tree species diversity data (species number, Simpson's diversity index and species evenness) were collated. This resulted in a distribution of 75 quadrats with 1–8 species present in the monodominant forest and that, with 7–24 species present in the mixed forest, was utilized to investigate the diversity-AGB growth relationship. The monodominant and mixed forests were analysed separately, because the two forest types had different trends in the diversity-AGB productivity relationship (see Chapter 4). The results of the pooled dataset from both forest types were presented for exploratory purposes only (Table 7.1).

A subset of ten quadrats in each study plot (i.e., a total of 30 quadrats for each forest type) was used to collect data on litterfall productivity and ANPP. Litterfall data was collected over one year to investigate the relationship between tree species diversity and temporal variability in litterfall biomass. Trap species number index (an indicator of species richness in the vicinity of the litterfall traps) was additionally available for this subset of quadrats in the study plots.

Table 7.1 A summary of the effects of tree species diversity on the ecosystem functions considered in this study.

Function tested	Effect along tree diversity gradient		
	Monodominant forest	Mixed forest	Pooled data from both forest types
AGB growth	?	Yes (+ve); significant	Yes* (+ve); significant (quadratic regression)
Litterfall productivity	?	Yes (+ve); significant	
ANPP	?	Yes (+ve); significant	
Temporal variation in litterfall biomass	Yes (-ve); significant	No	Yes (-ve); significant (cubic regression)
Decomposition rates:			
(1) Litterfall/standing crop ratio	Yes (+ve); not significant	Yes (+ve); not significant	Yes (+ve); significant (linear regression)
(2) Litterbag experiment			
Pure bay leaves	No	No	No
Mixed bay leaves	No	No	No
Pure <i>Gilbertiodendron</i> leaves	No	No	No
Mixed <i>Gilbertiodendron</i> leaves	Yes (+ve); ephemeral	No	No

“?” represents no clear pattern was detected, and this was probably due to data limitations and therefore warrant further research. * means the results were only for exploratory purposes.

The same subset of quadrats was used for the *in situ* litterbag experiments. The direct observations of decomposition rate (litterfall/standing crop ratio) consisted of a stratified-random design, with 3 quadrats situated in the monodominant forest and 3 in the mixed forest. Each of these quadrats was from a different study plot and this, fortuitously, resulted in a distribution of quadrats with 2–20 species present, utilized to investigate the relationship between tree diversity and litter decomposition. The following is the outline of the main findings and conclusions:

1. Monodominant forest dominated by *Gilbertiodendron dewevrei* had lower species richness than the mixed forest, even though the soil properties and climatic conditions of the two forest types were indistinguishable (Thesis objective 1, chapter 2; thesis objective 2, chapter 3).

Soil properties from the two forest types were not significantly different. Species richness of the successfully established non-dominant tree species (≥ 10 cm diameter in breast height [dbh]) in the monodominant forest of *Gilbertiodendron dewevrei* was compared with its adjacent mixed forest. Based on taxon sampling curves, my results provide evidence that the *Gilbertiodendron* forest had lower species richness, species density and population density than its adjacent mixed forests. I further examined the life-history traits of 58 species that had at least one individual with dbh ≥ 10 cm (i.e., successfully established) in the *Gilbertiodendron* forests. After controlling for phylogeny, the three most important determinants of the probability of successful establishment in the *Gilbertiodendron* forest were their relative abundance in the adjacent mixed forests, wood density and light requirement. The presence of a greater number of individuals in the mixed forest significantly increased the establishment success of tree species in the adjacent *Gilbertiodendron* forest. Also, shade-tolerant species with high wood density had a greater chance of establishing in the monodominant forest.

Future direction

This work demonstrates that some life history traits are influential in the successful establishment of tree species in the *Gilbertiodendron*-dominated forest. In order to further uncover the mechanisms that are regulating monodominance in tropical lowland forests, we should also examine the role of fauna as pollinators and seed dispersal agents. As in any pollination system by which the efficacy of animals as pollinators depends on the number of flowers visited and final deposition of pollens with a high probability of fertilization, the effectiveness of frugivores as seed dispersal agents of their food plants depends on the amount of fruit removal and the final deposition of seeds with a high probability of establishment (Jordano & Schupp 2000). Unsurprisingly, the functional efficiency of pollinators and seed dispersal agents, along with their diversity and abundance, is often considered to play a critical role in forest regeneration patterns and in the determination of forest regeneration dynamics (Moran et al. 2004). Therefore, future studies of monodominant forests and mixed forests, and their pollinators and seed dispersal agents may provide new insights into the comparative ecological stability of these forested systems, because animal activity is likely to have both demographic and evolutionary consequences for these ecosystems (Schupp, 1995).

2. Above-ground tree growth and fine litter productivity between the monodominant and mixed forests were similar; While tree species diversity had no effect on the forest AGB growth, fine litterfall productivity and ANPP in the monodominant forest, a positive diversity-tree growth relationship was found in the mixed forest (Thesis objective 3, chapter 4).

My study shows that the monodominant forests of *Gilbertiodendron dewevrei* had higher above-ground biomass than the mixed forests. However, the productivity (AGB production, litterfall productivity and ANPP) is not significantly different between the two forest types. Although tree diversity had no effect on AGB growth, litterfall productivity and ANPP in the monodominant forest, the above-ground biomass growth increased with more diverse tree communities in the mixed forest. The effect of diversity remained significant in the General

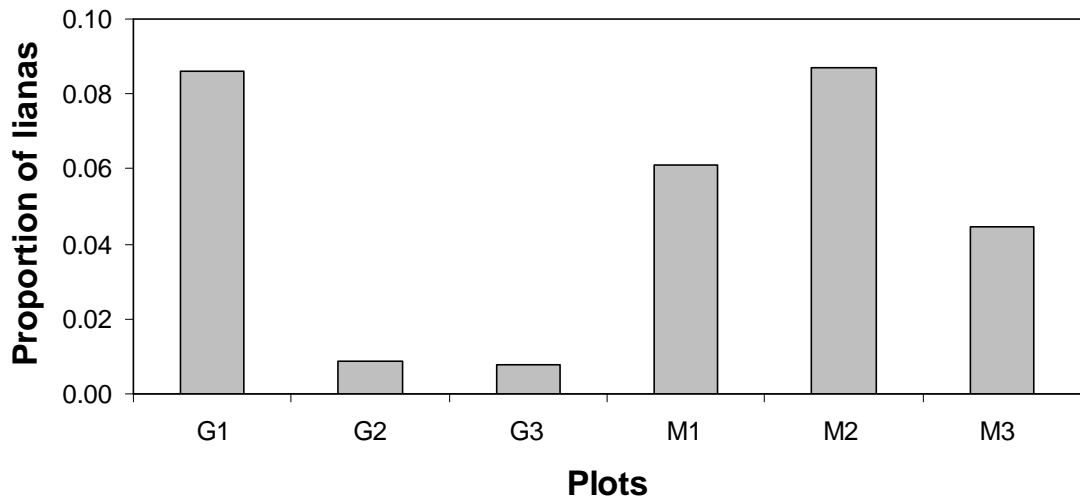
Linear Model (GLM) analyses of covariance where effects of stem density, spatial variation and quadrat biomass were controlled for. Litterfall productivity in the mixed forest was positively affected by the estimated plant species richness near the litterfall traps (trap species number). ANPP was also significantly increased with higher trap species number and was significant in the GLM analyses of covariance. This shows that the influence of the dominant *G. dewevrei* can be important in determining a system's overall ANPP, but diversity effects are important in the mixed forest.

Future direction

The influence of diversity on the ecosystem functioning in a tropical forest is especially poorly understood and, therefore, this study which relates tree species richness and diversity to AGB growth, litterfall productivity and ANPP in central African forest, contributes significantly to the scientific knowledge in the tropical forest ecology. However, a sampling regime by focusing on a large number of 20 m × 20 m plots (i.e., increasing number of replicates) stratified by species number will allow large-scale analysis of the relationship between ecosystem functions and diversity in tropical forests. In addition, using the whole RAINFOR and AFRITRON plots database (www.forestplots.net/) will enable the testing of this relationship on a global scale.

An area which needs attention is the effect of lianas on tree growth that are not taken into account in this work even though lianas were present in all plots of the monodominant and mixed forests. According to van der Heijden & Phillips (2009) working in South America, lianas can compete with trees and reduce the individual tree growth rates by 11 % yr⁻¹ on average, when all other variables that affect tree growth were accounted for. In the study site of that work, this average reduction per tree implies a reduction in tree growth of 0.49 Mg dry mass ha⁻¹ yr⁻¹ at the standing level. Although there is no evidence showing that a particular forest type in this study was more prone to be affected by the lianas (Fig. 7.1), lianas constituted 7 % of all stems ≥10 cm dbh in the mixed forest, whereas that was only 3 % in the monodominant forest. Therefore, this is a potential area for further research to determine the importance of lianas on the overall diversity-biomass productivity relationship of the forest.

Figure 7.1 The proportion of lianas (dbh ≥ 10 cm) found in each of six plots in 2005. G1–G3 are *Gilbertiodendron* forests; M1–M3 are adjacent mixed forests. For site details see Table 4.1.



3. Litterfall phenology was distinctively different between the monodominant and mixed forests; The magnitude of temporal variability of litterfall productivity was greater in monodominant forest than in mixed forest while an increasing diversity within the monodominant forest corresponded with decreasing temporary variability in litterfall productivity (Thesis objective 4, chapter 5).

Although total litterfall productivity between the monodominant and mixed forests was not significantly different, there was a major discrepancy between the two forest types in terms of absolute biomass of leaf and woody litterfall categories. The biomass of leaves and woody litter was higher in the mixed forest. Also, the mixed forests had a higher biomass allocation to woody litter although the biomass allocation to leaves was not significantly different between the two forest types. Three main litterfall peaks were observed in the monodominant forest: April, September and November, and total litterfall mass negatively correlated with temperature. The mixed forest had only two peaks in March–April and November for total litterfall but was not correlated with either rainfall or temperature. Increased diversity within the monodominant forest corresponded with decreased temporary variability in litterfall

productivity. However, the diversity had no effect on the temporal variability of litterfall productivity in the mixed forest where the magnitude of temporal variability was low at all levels of diversity present. I demonstrate that species richness independently affected temporal stability in the monodominant forest and its effect was not confounded by species composition. My results support previous findings of a positive relationship between diversity and temporal stability of ecosystem functioning.

Future direction

This study provides empirical evidence that higher stability in terms of temporal variation in litterfall productivity could be achieved by increasing tree species diversity. However, this finding was based on one year of data from the six 1 ha plots only. It is unclear if my results can be extrapolated to a larger scale because my study did not span all the variabilities in natural processes (e.g., masting) that are characteristics of realistic time and spatial scales. In view of such concern, Cardinale *et al.* (2004) used a patch-dynamic model which incorporates large scale processes of dispersal and disturbance to assess whether diversity effect is scale dependent or not. Their findings suggested that dispersal and disturbance amplified the diversity effect on functioning; and small-scaled experiments might not reflect the diversity-functioning relationship where large scale processes regulate species richness. Turning these findings around could mean that patterns underlying diversity-functioning relationship can be more pronounced at larger scale. Finally, using the same patch-dynamic model, Cardinale *et al.* (2004) concluded that diversity effect grows stronger with successional time; and the validity of diversity-functioning relationship is not affected by spatial scale per se. Nevertheless, (1) a sampling regime that focuses on a large number of 20 m × 20 m plots stratified by species number and (2) a meta-analysis of extant litterfall literature will allow a larger-scale analysis.

This work has been carried on for a second year and only total litterfall data was collected. Such a longer temporal scale has not only captured important events such as masting and non-masting periods, but has also encompassed a wider range of the annual variation in the

climate. My future analyses of this will further help in our understanding of the diversity-stability relationship in tropical forests.

4. The estimated decomposition rates, derived from litterfall/standing litter crop ratio, were not correlated with tree species diversity when the monodominant and mixed forests were analysed separately, but the decomposition rates were positively correlated with species diversity when the data was pooled from the two forest types; Litterbag experiments show that the positive litter mixing-effect might be ephemeral and context-dependent (Thesis objective 5, chapter 6).

The leaf-only litterfall production was significantly higher in the mixed forests. However, the litter standing crop was greater in the monodominant forests. Thus, the decomposition rate estimated using the litterfall/standing crop ratio in mixed forest was three times faster than that of monodominant forest. The estimated decomposition rates were correlated with tree species diversity only when the data from the two forest types was pooled together. A decomposition experiment was also carried out over nine months in the two forest types using mixed species litter bags containing two standard substrates—bay leaves (*Laurus nobilis*) and those of *Gilbertiodendron* sp.—and litter bags containing leaves of a single standard species. I found that the decomposition of bay leaves were faster than those of the *Gilbertiodendron* leaves and the decay rates for each of the standard species were the same in both forest types. Although *Gilbertiodendron* leaves did breakdown faster when mixed with the higher quality bay leaves after three months, the positive mixing-effect was short-lived and was not observed after five and nine months.

Future direction

This thesis attempts to study the effects of litter diversity on decomposition rates using two different methods: (1) a litterbag study in which the degradation of litterfall mixtures were compared to monocultures, and (2) a observational study comparing litterfall/litter standing

biomass along a tree diversity gradient. The findings confirm the results of some litterbag studies that report no effects of litter mixture on decomposition rates (Hättenschwiler *et al.* 2005). However, we still do not understand why the effect of litter diversity on decomposition rates is sometimes positive, negative or neutral (Hättenschwiler *et al.* 2005). Future research should, therefore, focus on the mechanisms that can explain the ambiguous litter diversity-decomposition rate studies. Furthermore, in the litterbag study, the highest diversity was two litter species only. But in tropical forests, including the Dja Faunal Reserve, litter diversity is significantly higher than two species. Therefore, there is a need to use more than two indigenous litter species to test the litter diversity-decomposition rate hypothesis.

7.2. Conservation implications

1. Insights for the management of timber extraction from *Gilbertiodendron dewevrei* forest.

The estimates of AGB and basal area of the monodominant *Gilbertiodendron* forest and its adjacent mixed forest imply that there is more volume of timber per hectare can be extracted from the monodominant forest as compared to the mixed forest (Chapter 4). As *G. dewevrei* is a valuable species for the local timber industry, my findings may have important implications for the management of monodominant *Gilbertiodendron* forest. Over-logging of *G. dewevrei* may substantially increase open areas and the colonization by species with low wood density (i.e., pioneer species). Hence, harvesting techniques and patterns that do not consider the ecological processes that underpin existing hardwood species distributions and abundances in the *Gilbertiodendron* forests will increase the risk of these species being replaced by those with lower-density wood. This will ultimately influence the availability of species with heavy wood, which is valuable for timber industry, in the monodominant forests. On the other hand, the monodominant forest with the highest dominance of *G. dewevrei* may not necessarily yield the highest AGB growth and basal area growth (see Table 4.1). This suggests that in the *Gilbertiodendron* forest, controlling the dominance of *G. dewevrei* may be a potential mechanism to optimize wood production.

2. Insights for the impacts of tree species loss on ANPP, and for improving current management practices in agroforestry and timber industry.

My finding suggests a positive relationship between tree diversity and the net primary production of tropical forested ecosystem (ANPP of the monodominant forest: 20.52 ± 3.04 Mg dry mass ha^{-1} ; ANPP of the mixed forest: 21.93 ± 2.05 Mg dry mass ha^{-1} ; see Chapter 4), and may have important implications for improving current management practices in agroforestry and timber industry. Selective loss of tree species in the tropical forest for specific uses (e.g., house-building, wood-carving, drum-making; Taylor *et al.* 2008) may result in a reduction in ANPP. In the Dja Faunal Reserve, species from genus *Uapaca* are selectively felled for local wood-carving activities. Based on my mixed forest data at the scale of $20 \text{ m} \times 20 \text{ m}$ quadrat, a regression of the change in quadrat species number on AGB growth yields this equation ($r^2 = 0.21$, $n = 75$; see Chapter 4):

$$\text{AGB growth} = (-0.0189 \times n_{\text{quadrat}}^2) + (0.8818 \times n_{\text{quadrat}}) - 3.9402$$

where n_{quadrat} is the quadrat species number. Another regression of the change in trap species number on ANPP yields the following equation ($r^2 = 0.12$, $n = 30$; see Chapter 4):

$$\text{ANPP} = (1.78 \times n_{\text{trap}}) - 1.24$$

where n_{trap} is the trap species number. In other words, for every loss of one trap species, ANPP is reduced by approximately $0.54 \text{ Mg dry mass ha}^{-1} \text{ yr}^{-1}$.

For practising agroforestry and selective logging in high-diversity African tropical forest, it is important to establish and to maintain forest tree communities with high species diversity in order to enhance long-term productivity. Furthermore, functioning of the low-diversity plantations (i.e., plant biomass production) and the resulting services (e.g., carbon sequestration) can be maximized using a high diversity of long-lived tree species.

At first glance, the results presented in Chapter 4 may imply that few dominant species are needed to maintain ecosystem processes. It is, however, important to preserve biodiversity for several reasons from a conservation perspective. First, we would still require a high diversity to ensure that the more productive species would have the highest probability of being included within systems. This is because for the most part, we do not know which species are of higher

functional importance. Second, it is unclear to what extent non-dominating species can fill the role of dominants that may have lower survival rate (Wills *et al.* 2006), or if functionally dominant species have the dispersal ability to ensure ecological processes across large spatial scales (Hillebrand & Blenckner 2002). Third, based on precautionary principle, 'low quality' species may fill new roles in ecosystem functioning in a changing environment. Candidate species being identified as dominant could be considered as 'high quality species' for their influence on these 'low quality' species and therefore be useful for preserving the integrity of a system (Hambler, 2004). Last, according to the 'insurance' argument, the species rich community is more stable than the species poor system because it is more likely to have some species in a high-diversity system to decompensate the negative effects on a certain species due to environmental fluctuations (Yachi & Loreau 1999).

3. Insights from the first demonstration of a positive diversity-stability relationship in a tropical forest.

McGrady-Steel *et al.* (1997) wrote that 'knowledge of ecosystem predictability facilitates effective ecosystem management by providing insights into potential temporal variation within systems, as well as possible spatial variation among comparable systems'. My study shows that the mixed forest was more stable than monodominant forest in terms of temporal variability in fine litterfall production. My observation of increased stability with increased diversity across both forest types is an encouraging indication of the conservation potential for tree species diversity. Although the diversity-stability relationship was not observed in the mixed forest, the magnitude of temporal variability in the mixed forest was low. The mixed forests may have species with largely redundant functional roles. But I emphasize that the maintenance of high biodiversity is still desirable because diversity may differently affect each ecological process and its variability (Hooper *et al.* 2005).

7.3. Recommendations of future work

Understanding monodominance in tropical forests

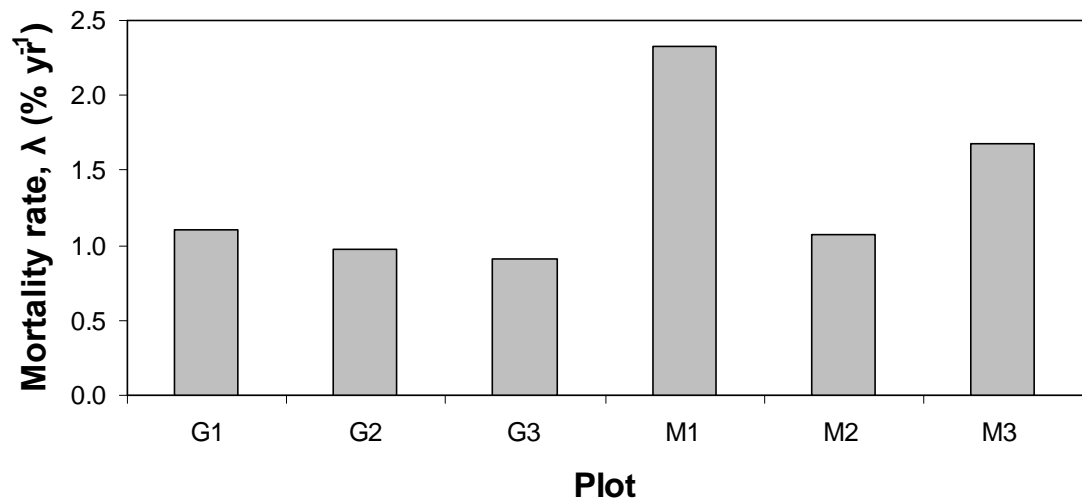
The basic ecology of the *Gilbertiodendron dewevrei* forest in central Africa is poorly understood. Although the findings of AGB growth, decomposition rate and the first estimates of litterfall productivity and ANPP of this monodominant forest presented in this thesis provide a significant development on the previous knowledge, we still do not fully understand the dynamics of this forest type and why they occur. Between 2005 and 2008, there were 30 dead trees found in the 3 ha monodominant forest, whereas 74 trees were found dead in the 3 ha mixed forest; the comparison of the mortality rates (λ), which is defined by $\lambda = [\ln(n_0) - \ln(n_t)]/t$ where n_0 and n_t are the initial stem number and the number of stems surviving to time t in yrs, respectively (Sheil & May 1996; Lewis *et al.* 2004b), among the six plots, showed that the monodominant forest consistently had lower tree mortality (Fig. 7.2). The mechanisms producing relatively lower mortality in the monodominant forest is unknown. Therefore, a framework for examining the mortality mechanisms in the monodominant forest and its adjacent mixed forest is needed. Understanding the dynamic of monodominant forest, together with the use of satellite images, will help to determine if the fragments of this forest type are expanding or shrinking in central Africa.

This thesis presents a conceptual framework that suggests possible interactions among previously assessed mechanisms to achieve classical monodominance (Chapter 1). However, rigorous testing of these interactions and feedbacks are required. The quantitative methodology of a meta-analysis will yield much more information than the qualitative review presented in this thesis. For example, a meta-analysis can combine the results of several studies that address the importance of various mechanisms to give a more accurate analysis. Further research on the roles of disturbances for monodominance, biogeographical history, physiological and life-history traits, and pollinators are also needed for a thorough evaluation of the framework.

The proposed mechanisms that promote monodominance do not make predictions as to whether classical monodominance by a specific species can persist over long time scales. In

fact, the critical question is whether monodominance for a particular landscape or locality is resistant to global change. To answer such a question, it may be necessary to consider the biogeographic history of the monodominant forest sites. This is because floristic history may reveal a possible past relationship between the dynamics of vegetation and the changes in the quality of environment, and hence provide clues as to how changes may occur in the future (Weng *et al.* 2006).

Figure 7.2 Mortality rate (λ) between 2005 and 2008 censuses in each of six plots. G1–G3 are *Gilbertiodendron* forests; M1–M3 are adjacent mixed forests. For site details see Table 4.1.



Fossil artefacts may contain information on past biodiversity. Therefore, fossil pollen from dated sediment cores obtained from monodominant landscapes could be a source of information on past patterns in floral richness and serve as a proxy for the reconstruction of diversity trend through time; thus uncovering the response of floristic diversity to environmental changes such as natural and anthropogenic disturbance, and diversification of landscapes. Improvements on current methods of measuring palynological richness (e.g. Weng *et al.* 2006) should enable us to answer some of the questions about the persistence of a particular classical monodominant forest sites and to make deductions. For example, if disturbance absence is crucial, we might expect classical monodominant stands not to persist for millennia at a particular site.

In general, monodominant forests must also be places where the usual diversity-enhancing mechanisms are not fully functional. Therefore, investigations of the mechanisms of monodominance may provide an alternative and complementary approach in the quest to understand why high levels of tree diversity are generally observed in tropical forests. Understanding the mechanisms that maintain diversity within tropical forests is an urgent task as the functioning of these ecosystems could be dependent on their biodiversity.

Understanding diversity-functioning relationship

The relations of tree species diversity to AGB growth, litterfall productivity and ANPP were presented in this thesis. However, the findings were derived from only six 1 ha forest plots. Although some modelling studies (e.g., Cardinale *et al.* 2004) have suggested that the diversity-productivity relationship is not influenced by spatial scale per se, it is uncertain if the positive relationship of mixed forest observed in the Dja Faunal Reserve can still hold at a larger spatial scale across the continent. A meta-analysis on the extensive empirical African forest data set (e.g., www.forestplots.net database) can aid in the validation if such positive relationship between productivity (AGB growth, litterfall productivity and ANPP) and tree species diversity can be extended to a regional level.

This thesis provides an insight on the mechanism that produced the diversity-productivity relationship in the monodominant *Gilbertiodendron* forest: the dominance effects of *G. dewevrei*, a species that occurs at high density of very large trees and high initial AGB. However, the mechanisms that are responsible for the positive associations between productivity and tree species diversity in the mixed forest are still unknown. In a synthetic high-diversity grassland community, both ‘sampling effects’ and complementarity were known to be not mutually exclusive (Tilman *et al.* 2001). Thus, it is interesting to find if the mechanisms producing the relationship of the highly diverse mixed forest includes both dominant species and a particular combination of species that are complementary. Therefore, further empirical studies, focussing on compositional effects (for ‘sampling effects’), biotic influences and abiotic environmental conditions (for complementarity in resource use), will help to determine the underlying mechanisms of the diversity-productivity relationship in the mixed forest.

The influence of plant functional diversity on ecosystem functions in the tropical forest is another interesting area for investigation. Despite a growing collection of studies on the effects of functional diversity on functioning, there is a surprisingly limited range of systems being investigated. These studies were conducted mostly in terrestrial grasslands and they found that functional diversity is an important determinant of local-scale ecosystem functioning (Petchey 2004). However, it is difficult to relate their results directly to ecosystems where species diversity is high, especially tropical forests. Extensive research on the importance of functional group richness on the forest functions would help to incorporate functional diversity effects in the ecosystem function assessments (Diaz *et al.* 2007).

Our knowledge of the world’s ecosystems can be substantially enhanced if we understand the exact contributions of individual species to ecosystem functioning and their responses to changes in environmental conditions. Large-scale species extinction in the tropics is largely inevitable over the coming century (Sodhi *et al.* 2004). Therefore, it is important to conserve as many species as possible and try to predict the directions of diversity effects on critical functions of all threatened ecosystems. However, the predictability of the relationship between diversity and functions is not only dependent on the type of biome, but also on the

response of the species involved to changing environments, and on their functional effect traits in relation to the ecosystem functions of concern. However, as a result of our limited basic knowledge of many tropical species' biology, the application of ecological concepts may be hindered, because basic natural history information is crucially missing. Ecologists need to study the basic physiological features and ecological traits of as many species within endangered ecosystems as possible. Perhaps our understanding of diversity-functioning relationship would vastly improve by acquiring knowledge from natural history studies.

References

- Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystem: a triangular relationship. *Oikos*, **79**, 439-449.
- Anderson, D.R. & Burnham, K.P. (2002) Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, **66**, 912-918.
- Anderson, J.A.R. (1961) The destruction of *Shorea albida* forest by an unidentified insect. *Empirical Forestry Review*, **40**, 19-29.
- Aragão, L.E.O.C., Malhi, Y., Metcalfe, D.B., Silva-Espejo, J.E., Jiménez, E., Navarrete, D., Almeida, A., Costa, A.C.L., Salinas, N., Phillips, O.L., Anderson, L.O., Baker, T.R., Goncalvez, P.H., Huamán-Ovalle, Mamani-Solórzano, M., Meir, P., Monteagudo, A., Peñuela, M.C., Prieto, A., Quesada, C.A., Rozas-Dávila, A., Rudas, A., Silva Junior, J.A. & Vásquez, R. (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, **6**, 2441-2488.
- Aoki, I. & Mizushima, T. (2001) Biomass diversity and stability of food webs in aquatic ecosystems. *Ecological Research*, **16**, 65-71.
- Bai, Y. F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181-184.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, J.N.M. & Martinez, R.V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545-562.
- Balvanera, P., Kremen, C. & Martínez-Ramos, M. (2005) Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecological Applications*, **15**, 360-375.
- Banasiak S.E. & Meiner S.J. (2009) Long term dynamics of *Rosa multiflora* in a successional system. *Biological Invasions*, **11**, 215-224

- Beard, J.S. (1946) The Mora forest of Trinidad, British West Indies. *Journal of Ecology*, **33**, 173-192.
- Bertness, M.D. & Ellison, A.M. (1987) Determinants of pattern in a New-England salt-marsh plant community. *Ecological Monographs*, **57**, 129-147.
- Blair, J.M., Parmelee, R.W. & Beare, M.H. (1990) Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology*, **71**, 1976-1985.
- Bolza, E. & Keating, W.G. (1972) *African timbers: the properties, uses and characteristics of 700 species*. Commonwealth Scientific and Industrial Research. Melbourne.
- Bond, E.M. & Chase, J.M. (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecology Letters*, **5**, 467-470.
- Boucher, D.H. (1981) Seed predation by mammals and forest dominance by *Quercus oleoides*, a tropical lowland oak. *Oecologia*, **49**, 409-414.
- Bradshaw, C.J.A., Navjot, N.S. & Brook, B.W. (2009) Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and Environment*, **7**, 79-87.
- Brady, N.C. & Weil, R.R. (1999) *The nature of properties of soils*. 12th edition, Prentice Hall, New Jersey.
- Brown, S. (1997) *Estimating biomass and biomass change of tropical forests – a primer*. FAO Forestry Paper No. 134. FAO, Rome.
- Brüinig, E.F. (1974) *Ecological studies in the Kerangas forests of Sarawak and Brunei*. Borneo Literature Bureau for Sarawak Forest Department, Kuching.
- Bunker, D.E., de Clerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M. & Naeem, S. (2005) Species loss and above-ground carbon storage in a tropical forest. *Science*, **310**, 1029-1031.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference. A Practical Information-theoretic Approach*. Springer-Verlag New York Inc, New York.
- Butler, R.A. (2006) *The Amazon: the world's largest rainforest*.
<http://rainforests.mongabay.com/0103.htm>.

- Cardinale, B.J., Ives, A.R. & Inchausti, P. (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos*, **104**, 437-450.
- Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000) Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, **91**, 175-183.
- Carpenter, S.R. & Lodge, D.M. (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, **26**, 341-370.
- Caspersen, J.P. & Pacala, S.W. (2001) Successional diversity and forest ecosystem function. *Ecological Research*, **16**, 895-903.
- Cassey, P., Blackburn, T.M., Duncan, R.P. & Lockwood, J.L. (2008) Lessons from introductions of exotic species as a possible information source for managing translocation of birds. *Wildlife Research*, **35**, 193-201.
- Chao, K.J., Phillips, O.L., Gloor, E., Monteagudo, A., Torres-Lezama, A. & Martinez, R.V. (2008) Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*, **96**, 281-292.
- Chapman, K., Whittaker, J.B. & Heal, O.W. (1988) Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agricultural Ecosystem and Environment*, **24**, 33-40.
- Chatterjee, S., Hadi, A.S. & Price, B. (2000) *Regression analysis by example*. 3rd edition, Wiley, New York
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009a) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351-366.
- Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L.E.O.C., Bonal, D., Châtelet, P., Silva Espejo, J., Goret, J.-Y., von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M.C., Phillips, O.L., Stevenson, P. & Malhi, Y. (2009b) Regional and temporal patterns of litterfall in tropical South America. *Biogeosciences Discussions*, **6**, 7565-7597.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H.,

- Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.
- Chave, J., Olivier, J., Bongers, F., Chatelet, P., Forget, P.M., van der Meer, P., Norden, N., Riera, B. & Charles-Dominique, P. (2008) Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology*, **24**, 355-366.
- Clark, D.A. & Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist*, **124**, 769-788.
- Clark, D.A. & Clark, D.B. (1992) Life-history diversity of canopy and emergent trees in a neotropical rain-forest. *Ecological Monographs*, **62**, 315-344
- Clark, D.A., Clark, D.B., Sandoval, R. & Castro, M.V. (1995) Edaphic and human effects on landscape-scale distributions of tropical rain-forest palms. *Ecology*, **76**, 2581-2594.
- Clark, D.A., Brown S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. & Holland, E.A. (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371-384.
- Colwell, R.K. (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, **345**, 101-118
- Connell, J.H. & Lowman, M.D. (1989) Low-diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist*, **134**, 88-119.
- Conway, D. (1992) *A comparison of soil parameters in monodominant and mixed forest in the Ituri Forest Reserve, Zaire*. Tropical Environmental Science Honours Project. University of Aberdeen, Aberdeen.
- Coomes, D.A. & Grubb, P.J. (1996) Amazonian caatinga and related communities at La Esmeralda, Venezuela: forest structure, physiognomy and floristics, and control by soil factors. *Vegetatio*, **122**, 167-191.

- Coomes, D.A. & Grubb, P.J. (1998) A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Functional Ecology*, **12**, 426-435.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, **4**, 72-85.
- Coûteaux, M.M., Bottner, P. & Berg, B. (1995) Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution*, **10**, 63-66.
- Daly, D.C. & Mitchell, J.D. (2000) Lowland vegetation of tropical South America – an overview. In: Lentz, D. (ed.) *Imperfect balance: Landscape transformation in the pre-Columbian Americas*, pp. 391-454. Columbia University Press, New York, USA.
- DeMott, W.R. (1998) Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology*, **79**, 2463-2481.
- Diaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of National Academy of Sciences*, **104**, 20684-20689.
- Didham, R.K. (1998) Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia*, **116**, 397-406.
- Diehl, S. (1993) Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos*, **68**, 151-157.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist*, **151**, 264-276.
- Downing, A.L. & Leibold, M.A. (2002) Ecosystem consequences of species richness and composition in pond food webs. *Nature*, **416**, 837-841.
- Duarte, P., Macedo, M.F. & da Fonseca, L.C. (2006) The relationship between phytoplankton diversity and community function in a coastal lagoon. *Hydrobiologia*, **555**, 3-18.
- Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201-219.

- Duffy, J.E., Richardson, J.P. & Canuel, E.A. (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, **6**, 637-645.
- Duffy, J.E., Richardson, J.P. & France, K.E. (2005) Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters*, **8**, 301-309.
- Dupain, J., Guislain, P., Nguenang, G.M., de Vleeschouwer, K. & Van Elsacker, L. (2004) High chimpanzee and gorilla densities in a non-protected area on the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx*, **38**, 209-216.
- Eggeling, W.J. (1947) Observations on the ecology of Budongo rain forest, Uganda. *Journal of Ecology*, **34**, 20-87.
- Engelhardt, K.A.M. & Ritchie, M.E. (2002) The effect of aquatic plant species richness on wetland ecosystem processes. *Ecology*, **83**, 2911-2924.
- Erskine, P.D., Lamb, D. & Bristow, M. (2006) Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management*, **233**, 205-210.
- Fang, Z.X. & Bailey, R.L. (1998) Height-diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management*, **110**, 315-327.
- Finke, D.L. & Denno, R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, **8**, 1299-1306.
- Foster, S.A. & Janson, C.H. (1985) The relationship between seed size and establishment conditions in tropical woody plants. *Ecology*, **66**, 773-780.
- Forget P.-M. (1989) La régénération naturelle d'une espèce autochore de la forêt Guyanaise: *Eperua falcate* Aublet (Casalpiniaceae). *Biotropica*, **21**, 115-121.
- Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005). Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecology Letters*, **8**, 696-703.
- Gartner, B.L. (1989) Breakage and regrowth of *Piper* species in rain-forest understory. *Biotropica*, **21**, 303-307.

- Gessner, M.O., Inchausti, P., Persson, L., Raffaelli, D.G. & Giller, P.S. (2004) Biodiversity effects on ecosystem functioning: insights from aquatic systems. *Oikos*, **104**, 411-422.
- Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, E.M. & Parton, W.J. (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, **6**, 751-765.
- Giller, P.S., Hillebrand, H., Berninger, U.-G., Gessner, M.O., Hawkins S., Inchausti P., Inglis, C., Leslie, H., Malmqvist, B., Monaghan, M.T., Morin, P.J. & O'Mullan, G. (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos*, **104**, 423-436.
- Gonzalez, A. & Chaneton, E.J. (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *Journal of Animal Ecology*, **71**, 594-602.
- González, G. & Seastadt, T.R. (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology*, **82**, 955-964.
- Gotelli, N.J., Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.
- Gough, L., Grace, J.B. & Taylor, K.L. (1994). The Relationship between Species Richness and Community Biomass - the Importance of Environmental Variables. *Oikos*, **70**, 271-279.
- Gross, K. & Cardinale, B.J. (2005). The functional consequences of random vs. ordered species extinctions. *Ecology Letters*, **8**, 409-418.
- Gross, N.D., Torti, S.D., Feener Jr., D.H. & Coley, P.D. (2000). Monodominance in an African rain forest: Is reduced herbivory important? *Biotropica*, **32**, 430-439.
- Grubb, P.J., Turner, I.M. & Burslem, D.F.R.P. (1994). Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: analysis of soil, leaves and litter. *Journal of Tropical Ecology*, **10**, 559-577.
- Hambler, C. (2004). *Conservation*. Cambridge Press, Cambridge.
- Hammond, D.S. & Brown, V.K. (1998) Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings.

- In: Newbery, D.M., Prins, H.H.T. & Brown, N.D. (eds) *Dynamics of tropical communities*, pp. 51-78. Blackwell Science, Oxford.
- Harcourt, A.H., Coppeto, S.A. & Parks, S.A. (2002) Rarity, specialization and extinction in primates (vol 29, pg 445, 2002). *Journal of Biogeography*, **29**, 1717-1717
- Hart, T.B. (1985) *The ecology of a single-species-dominant forest and of a mixed forest in Zaire, Africa*. Ph.D. Thesis. Michigan State University, USA.
- Hart, T.B. (1995) Seed, seedling and sub-canopy survival in monodominant and mixed forests of the Ituri Forest, Africa. *Journal of Tropical Ecology*, **11**, 443-459.
- Hart, T.B., Hart, J.A. & Murphy, P.G. (1989) Monodominant and species-rich forests in the humid tropics: causes for their co-occurrence. *American Naturalist*, **133**, 613-633.
- Hättenschwiler, S. & Gasser, P. (2005) Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, **102**, 1519-1524.
- Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology & Evolution Systems*, **36**, 191-218.
- Heal, O.W., Anderson, J.M. & Swift, M.J. (1997) Plant litter quality and decomposition: an historical overview. In: Cadish, G. & Giller, K.E. (eds) *Driven by nature: plant litter quality and decomposition*, pp3-32. CAB International.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123-1127.
- Hector, A., Beale, A.J., Minns, A., Otway, S.J. & Lawton, J.H. (2000) Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos*, **90**, 357-371.

- Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A. & Haines, B.L. (1999) Soil microarthropod contributions to decomposition dynamics: Tropical-temperate comparisons of a single substrate. *Ecology*, **80**, 1873-1882.
- Henkel, T.W., Mayor, J.R. & Woolley, L.P. (2005) Masting fruiting and seedling survival of the ectomycorrhizal, monodominant *Dicymbe corymbosa* (Caesalpinaceae) in Guyana. *New Phytologist*, **167**, 543-556.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.
- Hillebrand, H. & Cardinale, B.J. (2004) Consumer effects decline with prey diversity. *Ecology Letters*, **7**, 192-201.
- Hillebrand, H. & Blenckner, T. (2002) Regional and local impact on species diversity – from pattern to processes. *Oecologia*, **132**, 479-491.
- Hillebrand, H. & Kahlert, M. (2001) Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. *Limnology and Oceanography*, **46**, 1881-1898.
- Hodgson, D.J., Rainey, P.B. & Buckling, A. (2002) Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 2277-2283.
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. (1971) *Forest environments in tropical life zones*. Pergamon Press, Oxford.
- Holm, J.A., Miller, C.J. & Copper Jr., W.P. (2008) Population dynamics of the dioecious Amazonian palm *Mauritia flexuosa*: simulation analysis of sustainable harvesting. *Biotropica*, **40**, 550-558.
- Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302-1305.
- Hooper, D.U., Chaplin, III, S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,

- Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.
- Hopkins, B. (1966) Vegetation of Olokemeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to the seasonal changes. *Journal of Ecology*, **54**, 687-703.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201-228.
- Hubbell, S.P. (2004) Two decades of research on the BCI Forest dynamics plot. In: Losos, E.C. & Leigh Jr., E.G. (eds) *Tropical forest diversity and dynamism: findings from a large-scale plot network*, pp. 8-30. University of Chicago, Chicago.
- Hubbell, S.P. & Foster, R.B. (1986) Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soule, ME (ed) *Conservation biology: The science of scarcity and diversity*, pp 205-231. Sinauer Associates, Sunderland.
- Hughes, R.H & Hughes, J.S. (1992) A directory of African wetlands. IUCN, UNEP and WCMC.
- Huston, M. A. (1997) Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449-460.
- Interlandi, S.J. & Kilham, S.S. (2001) Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology*, **82**, 1270-1282.
- Ithoh, A. (1995). Effects of forest floor environment on germination and seedling establishment of two Bornean rainforest emergent species. *Journal of Tropical Ecology*, **11**, 517-527.
- Ives, A.R. & Cardinale, B.J. (2004) Food-web interactions govern the resistance of communities after non-random extinctions. *Nature*, **429**, 174-177.
- Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, **317**, 58-62.
- Jablonski, D. (1991) Extinctions - a paleontological perspective. *Science*, **253**, 754-757.
- Janzen, D.H. (1974) Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica*, **6**, 69-103.

- Janzen, D.H. (1978) Description of a *Pterocarpus officinale* (Leguminosae) monoculture in Corcovada National Park, Costa Rica. *Brenesia*, **14-15**, 305-309.
- Jenny, H.G., Gessel, S.P. & Bingham, F.T. (1949) Comparative study of decomposition of organic matters in temperate and tropical regions. *Soil Sciences*, **68**, 419-432.
- Johnston, M. & Gillman, M. (1995) Tree population studies in low-diversity forests, Guyana I. Floristic composition and stand structure. *Biodiversity and Conservation*, **4**, 339-362.
- Jones, M.J., Sullivan, M.S., Marsden, S.J. & Linsley, M.D. (2001) Correlates of extinction risk of birds from two Indonesian islands. *Biological Journal of the Linnean Society*, **73**, 65-79.
- Jonsson, M. (2006) Species richness effects on ecosystem functioning increase with time in an ephemeral resource system. *Acta Oecologica-International Journal of Ecology*, **29**, 72-77.
- Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: The quality component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591-615.
- Keeling, H.C. & Phillips, O.L. (2007) The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, **16**, 618-631.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*, **32**, 1107-1116.
- Kiessling, W. (2005) Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs. *Nature*, **433**, 410-413.
- Kutbay, H.G. (2000) Sclerophylly in *Franxinus angustifolia* Vahl. subsp. *oxycarpa* (Bieb.ex Willd.) Fanco & Rocha Afonso and *Laurus nobilis* L. and edaphic relations of these species. *Turkish Journal of Botany*, **24**, 113-119.
- Kyereh, B., Swaine, M.D. & Thompson, J. (1999) Effect of light on the germination of forest trees in Ghana. *Journal of Ecology*, **87**, 772-783.
- Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**, 538-547.

- Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., Toutain, F., Barois, I., Schaefer, R. (1993) A hierarchical model for decomposition in terrestrial ecosystems; application to soils of the humid tropics. *Biotropica*, **25**, 130-150.
- Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, **12**, 474-478.
- Leibold, M.A. (1997) Do nutrient-competition models predict nutrient availabilities in limnetic ecosystems? *Oecologia*, **110**, 132-142.
- Leigh Jr., E.G. (1999) *Tropical forest ecology. A view from Barro Colorado island*. Oxford University Press, Oxford.
- Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, K.M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. & Wöll, H. (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, 1003-1007.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Lezama, A.T., Martinez, R.V., Brown, S., Chave, J., Kuebler, C., Vargas, P.N. & Vinceti, B. (2004a) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 421-436.
- Lewis, S.L., Phillips, O.L., Sheil, D., Vinceti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Vargas, P.N., Sonké, B., Nur Supardi, M.N., Terborgh, J.W. & Martínez, R.V. (2004b) Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census interval vary. *Journal of Ecology*, **92**, 929-944.

- Liow, L.H. (2000) Mangrove conservation in Singapore: A physical or a psychological impossibility? *Biodiversity and Conservation*, **9**, 309-332.
- Liu, K., Eastwood, R.J., Flynn, S., Turner, R.M. & Stuppy, W.H. (2008) Seed information database. <http://www.kew.org/data/sid>
- Loehle, C. (1988) Tree life-history strategies – the role of defenses. *Canadian Journal of Forest Research*, **18**, 209-222.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, **91**, 3-17.
- Loreau, M. (2004) Does functional redundancy exist? *Oikos*, **104**, 606-611.
- Loreau, M., & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiment. *Nature*, **412**, 72-76.
- Loreau, M., Mouquet, N. & Gonzalez, A. (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*, **100**, 12765-12770.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, **294**, 804-808.
- Loreau, M., Naeem, S. & Inchausti, P. (2002) *Biodiversity and ecosystem functioning: Synthesis and perspectives*. Oxford University Press, Oxford.
- Lyons, K.G. & Schwartz, M.W. (2001) Rare species loss alters ecosystem function - invasion resistance. *Ecology Letters*, **4**, 358-365.
- Madritch, M.D. & Cardinale, B.J. (2007) Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: a multi-site experiment along a latitudinal gradient. *Plant Soil*, **292**, 147-159.
- Maisels, F. (2004) Defoliation of a monodominant rain-forest tree by a noctuid moth in Gabon. *Journal of Tropical Ecology*, **20**, 239-241.

- Makana, J.-R., Terese, B.H., Hibbs, D.E. & Condit, R. (2004a) Stand structure and species diversity in the Ituri forest dynamics plots: a comparison of monodominant and mixed forest stands. In Losos, E.C. & Leigh Jr., E.C. (eds) *Tropical forest diversity and dynamism*, pp 159-174. University of Chicago Press, Chicago.
- Makana, J.-R., Terese, B.H., Liengolaa, I., Ewango, C., Hart, J.A. & Condit, R. (2004b) Ituri forest dynamics plots, Democratic republic of Congo. In Losos, E.C. & Leigh Jr., E.C. (eds) *Tropical forest diversity and dynamism*, pp 492-505. University of Chicago Press, Chicago.
- Margaris, N.S., Adamandiadou, S., Siafaca, L. & Diamantopoulos, J. (1984) Nitrogen and phosphorous content in plant species of Mediterranean ecosystems in Greece. *Vegetatio*, **55**, 29-35.
- Marimon, B.S., Felfili, J.M. & Haridasan, M. (2001) Studies in monodominant forests in eastern Mato Grosso, Brazil: I. A forest of *Brosimum rubescens* Taub.. *Edinburgh Journal of Botany*, **58**, 123-137.
- Martijena, N.E. (1998) Soil properties and seedling establishment in soils from monodominant and high-diversity stands of the tropical deciduous forests of Mexico. *Journal of Biogeography*, **25**, 707-719.
- McGinley, M. (2008) Dja Faunal Reserve. In Cleveland, C.J. (ed) *Encyclopedia of Earth*. United Nations Environment Programme–World Conservation Monitoring Centre. http://www/eoearth.org/article/Dja_Faunal_Reserve,_Cameroon
- McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997) Biodiversity regulates ecosystem predictability. *Nature*, **390**, 162-165.
- McGuire, K.L. (2007) Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. *Ecology*, **88**, 567-574.
- Medina, E., Garcia, V. & Cuevas, E. (1990) Sclerophyll and oligotrophic environments: relationships between leaf structure, mineral nutrient content and drought resistance in tropical rain forests of the Upper Rio Negro. *Biotropica*, **22**, 51-64.

- Meetenmeyer, V. (1984) The geography of organic decomposition rates. *Annals of the Association of American Geographers*, **74**, 551-560.
- Menard, S. (2002) *Applied logistic regression analysis*. Sage University Papers Series on Quantitative Applications in the Social Sciences, series no 07-106. Sage, California.
- Mesquita, R., De C.G., Workman, S.W. & Neely, C.L. (1998) Slow litter decomposition in a *Cecropia*-dominated secondary forest of central Amazonia. *Soil Biology and Biochemistry*, **30**, 167-175.
- Molloy, L. & Hart, J.A. (2002) Duiker food selection: Palatability trials using natural foods in the Ituri forest, Democratic Republic of Congo. *Zoo Biology*, **21**, 149-159.
- Moore, D.R.J. & Keddy, P.A. (1989) The relationship between species richness and standing crop in wetlands - the importance of scale. *Vegetatio*, **79**, 99-106.
- Moran, C., Catterall, C.P., Green, R.J. & Olsen, M.F. (2004) Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia*, **141**, 584-595.
- Morin, P.J. & McGrady-Steed, J. (2004) Biodiversity and ecosystem functioning in aquatic microbial systems: a new analysis of temporal variation and species richness-predictability relations. *Oikos*, **104**, 458-466.
- Mueller-Dombois, D. (2000) Rain forest establishment and succession in Hawaiian Islands. *Landscape and Urban Planning*, **51**, 147-157.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001) Physical stress and diversity-productivity relationships: The role of positive interactions. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 6704-6708.
- Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20-32.
- Murphy, J. & Riley J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31-36.
- Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature*, **390**, 507-509.
- Naeem, S., Hahn, D.R. & Schuurman, G. (2000) Producer-decomposer co-dependency

- influences biodiversity effects. *Nature*, **403**, 762-764.
- Naeem, S., Loreau, M. & Inchausti, P. (2002) Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. In Loreau, M., Naeem, S., & Inchausti, P. (eds). *Biodiversity and ecosystem functioning: Synthesis and perspectives*, pp3-17. Oxford University Press, Oxford.
- Naeem, S., Hahn, D.R. & Schuurman, G. (2000) Producer-decomposer co-dependency influences biodiversity effects. *Nature*, **403**, 762-764.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737.
- Nascimento, M.T., Barbosa, R.I., Villela, D.M. & Proctor, J. (2007) Above-ground biomass changes over an 11-year period in an Amazon monodominant forest and two other lowland forests. *Plant Ecology*, **192**, 181-191.
- Nascimento, M.T. & Proctor, J. (1997a) Population dynamics of five tree species in a monodominant *Peltogyne* forest and two other forest types on Maraca Island, Roraima, Brazil. *Forest Ecology and Management*, **94**, 15-128.
- Nascimento, M.T. & Proctor, J. (1997b) Soil and plant changes across a monodominant rain forest boundary on Maraca Island, Roraima, Brazil. *Global Ecology and Biogeography Letters*, **6**, 387-395.
- Nelson, B.W, Kapos, V., Adams, J.B., Oliveira, W.J., Braun, O.P.G. & do Amaral, I.L. (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology*, **75**, 853-858.
- Newbery, D.M., van der Burgt, X.M. & Moravie, M.-A. (2004) Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* trees in central African rain forest: the possible role of periods of multiple disturbance events. *Journal of Tropical Ecology*, **20**, 131-143.
- Newbery, D.M., Alexander, I.J. & Rother, J.A. (1997) Phosphorus dynamics in a lowland African rain forest: The influence of ectomycorrhizal trees. *Ecological Monographs*, **67**, 367-409.

- Parmentier, I., Malhi, Y., Senterre, B., Whittaker, R.J., A.T.D.N., Alonso, A., Balinga, M.P.B., Bakayoko, A., Bongers, F., Chatelain, C., Comiskey, J., Cortay, R., Djuikouo Kamdem, M.-N., Doucet, J.-L., Gautier, L., Hawthorne, W.D., Issembe, Y.A., Kouamé, F.N., Kouka, L.A., Leal, M.E., Lejoly, J., Lewis, S.L., Nusbaumer, L., Parren, M., Peh, K.S.-H., Phillips, O.L., Poorter, L., Sheil, D., Sonké, B., Sosef, M.S.M., Sunderland, T.C.H., Stropp, J., ter Steege, H., Swaine, M.D., Tchouto, M.G.P., van Gemerden, B.S., van Valkenburg, J.L.C.H. & Wöll, H. (2007) The odd man out? Might climate explain the lower tree α -diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology*, **95**, 1058-1071.
- Parolin, P., Oliverira, A.C., Piedade, M.T.F., Wittmann, F. & Junk, W.J. (2002) Pioneer trees in Amazonian floodplains: three key species form monospecific stands in different habitats. *Folia Geobotanica*, **37**, 225-238.
- Penuelas, J. & Estiarte, M. (1997) Trends in plant carbon concentration and plant demand for N throughout this century. *Oecologia*, **109**, 69-73.
- Petchey, O.L. (2004) On the statistical significance of functional diversity effects. *Functional Ecology*, **18**, 297-303.
- Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6-18.
- Phillips, O.L. & Baker, T. (2002) *Field manual for plot establishment and remeasurement*. RAINFOR Amazon forest inventory network.
- Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Vásquez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of National Academy of Science USA*, **91**, 2805-2809.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347-350.
- Pleysier, J.L. & Juo, S.R. (1980) A single extraction method using silver-thiourea for measuring exchangeable cations and effective CEC in soils with variable charges. *Soil Science*, **129**, 205-211.

- Polley, H.W., Wilsey, B.J. & Derner, J.D. (2003) Do species evenness and plant diversity influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecology Letters*, **6**, 248-256.
- Poorter, L., Bongers, F., Sterck, F.J. & Wöll, H. (2003) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, **84**, 602-608
- Poorter, L., Bongers, F., Sterck, F.J. & Wöll H. (2005) Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology*, **93**, 256-267.
- Powers, J. & Montgomery, R. (2006) The joint influences of climate, litter quality and soil fauna in regulating above- and belowground decomposition processes: a pan-tropical study. <http://life.bio.sunysb.edu/ee/powers/Decomposition%20in%20Tropical%20Forests.htm>
- Proctor, J., Anderson, J.M., Fogden, S.C.L. & Vallack, H.W. (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop and preliminary observations on herbivory. *Journal of Ecology*, **71**, 261-283.
- Purvis, A., Agapow, P.M., Gittleman, J.L. & Mace, G.M. (2000) Nonrandom extinction and the loss of evolutionary history. *Science*, **288**, 328-330.
- Quesada, C.A. (2009) *Soil vegetation interaction across Amazonia*. Ph.D. thesis, University of Leeds, Leeds.
- Read, J., Jaffre, T., Ferris, J.M., McCoy, S. & Hope, G.S. (2006) Does soil determine the boundaries of monodominant rain forest with adjacent mixed rain forest and maquis on ultramafic soils in New Caledonia? *Journal of Biogeography*, **33**, 1055-1066.
- Read, J., Jaffre, T., Godrie, E., Hope, G.S. & Veillon, J.-M. (2000) Structural and floristic characteristics of some monodominant and adjacent mixed rainforests in New Caledonia. *Journal of Biogeography*, **27**, 233-250.
- Reich, P.B., Tilman, D., Naeem, S., Ellsworth, D.S., Knops, J., Craine, J., Wedin, D. & Trost J.

- (2004) Species and functional group diversity independently influence biomass accumulation and its response to CO₂ and N. *Proceedings of the National Academy of Sciences*, **101**, 10101-10106.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.
- Richards, P.W. (1996) The tropical rain forest. 2nd ed. Cambridge University Press, Cambridge.
- Rijsdijk, J.F. & Laming, P.B. (1994) *Physical and related properties of 145 timbers*. Kluwer Academic, Dordrecht.
- Rubinstein, A. & Vasconcelos, H.L. (2005) Leaf-litter decomposition in Amazonian forest fragments. *Journal of Tropical Ecology*, **21**, 699-702.
- Scherer-Lorenzen, M. (2008) Functional diversity affects decomposition processes in experimental grasslands. *Functional Ecology*, **22**, 547-555.
- Scherer-Lorenzen, M., Bonilla, J.L. & Potvin, C. (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos*, **116**, 2108-2124.
- Schläpfer, F., Pfisterer, B. & Schmid, B. (2005) Non-random species extinction and plant production: implications for ecosystem functioning. *Journal of Applied Ecology*, **42**, 13-24.
- Schlesinger, W.H. (1991) *Biogeochemistry: an analysis of global change*. Academic Press, San Diego.
- Schmid, B. & Hector, A. (2004) The value of biodiversity experiments. *Basic and Applied Ecology*, **5**, 535-542.
- Schöngart, J., Piedade, M.T.F., Wittmann, F., Junk, W.J. & Worbes, M. (2005) Wood growth patterns of *Macaranga acaciifolia* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. *Oecologia*, **145**, 454-461.
- Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399-409.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & van Mantgem,

- P.J. (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, **122**, 297-305.
- Sheil, D. & May, R.M. (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology*, **84**, 91-100.
- Silver, W.L. & Miya, R.K. (2001) Global patterns in root decomposition: comparisons of climate and litter quality. *Oecologia*, **129**, 407-419.
- Sim, J.W.S., Tan, H.T.W. & Turner, I.M. (1992) *Adinandra belukar*: an anthropogenic heath forest in Singapore. *Vegetatio*, **102**, 125-137.
- Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non random species loss. *Ecology Letters*, **6**, 509-517.
- Sodhi, N.S., Liow, L.H. & Bazzaz, F.A. (2004) Avian extinctions from tropical and subtropical forests. *Annual Review of Ecology Evolution and Systematics*, **35**, 323-345.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.S. (2004) Extinction and ecosystem function in the marine benthos. *Science*, **306**, 1177-1180.
- Songwe, N.C., Fasehun, F.E. & Okali, D.U.U. (1988) Litterfall and productivity in a tropical rain forest, South Bakundu Forest Reserve, Cameroon. *Journal of tropical Ecology*, **4**, 25-37.
- Sonké, B. (2004) Forêts de la réserve du Dja (Cameroun): études floristiques et structurales. *Scripta Botanica Belgica*, **32**. Jardin Botanique National de Belgique, Bruxelles
- Sonké, B. (1998) *Etudes floristiques et structurales des forêts de la réserve de faune du Dja (Cameroun)*. PhD thesis, Université Libre de Bruxelles, Brussels.
- SPSS. (2006) *SPSS 15.0 for windows*. SPSS Inc., Chicago.
- Srivastava, D.S. & Vellend, M. (2005) Biodiversity-ecosystem function research: Is it relevant to Conservation? *Annual Reviews in Ecology, Evolution and Systematics*, **36**, 267-294.
- Steiner, C.F. (2001) The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. *Ecology* **82**:2495-2506.

- Steiner, C.F., Long, Z.T., Krumins, J.A. & Morin, P.J. (2005) Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecology Letters*, **8**, 819-828.
- Symstad, A.J., Chaplin, III, S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittelbach, G.G., Peters, D.P.C. & Tilman, D. (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience*, **53**, 89-98.
- Taylor, D., Hamilton, A.C., Lewis S.L. & Nantale G. (2008) Thirty-eight years of change in a tropical forest: plot data from Mpanga Forest Reserve, Uganda. *African Journal of Ecology*, **46**, 655-667.
- ter Steege, H. & Hammond, D.S. (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*, **82**, 3197-3212.
- Thébault, E. & Loreau, M. (2005) Trophic interactions and the relationship between species diversity and ecosystem stability. *American Naturalist*, **166**, E95-E114.
- Thompson, K., Askew A.P., Grime, J.P., Dunnet, N.P. & Willis, A.J. (2005) Biodiversity, ecosystem function and plant traits in mature and immature plant communities. *Functional Ecology*, **19**, 355-358.
- Tilman, D. (1999a) Diversity and production in European grasslands. *Science*, **286**, 1099-1100.
- Tilman, D. (1999b) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455-1474.
- Tilman, D. & Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363-365.
- Tilman, D., Knops, J., Wedin, D. & Reich P. (2002) Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands. In Loreau, M., Naeem, S. & Inchausti, P. (eds) *Biodiversity and ecosystem functioning: Synthesis and perspectives*, pp 21-35. Oxford University Press, Oxford.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: theoretical consideration. *Proceedings of the National Academy of Sciences*, **94**, 1857-1861.

- Tilman, D., Reich, P., Knops, J., Wedin, D., Mielke, T. & Lehman, C.L. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843-845.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629 – 632.
- Torti, S.D & Coley, P.D. (1999) Tropical monodominance: a preliminary test of the ectomycorrhizal hypothesis. *Biotropica*, **31**, 220-228.
- Torti, S.D., Coley, P.D. & Janos, D.P. (1997) Vesicular-arbuscular mycorrhizae in two tropical monodominant tree species. *Journal of Tropical Ecology*, **13**, 623-629.
- Torti, S.D., Coley, P.D. & Kursar, T.A. (2001) Causes and consequences of monodominance in tropical lowland forests. *American Naturalist*, **157**, 141-153.
- Turner, I.M. (2001) *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge.
- Valone, T.J. & Barber, N.A. (2008) An empirical evaluation of the insurance hypothesis in diversity-stability models. *Ecology*, **89**, 522-531.
- van der Heijden, G.M.F. & Phillips, O.L. (2009) Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, **6**, 2217-2226.
- van der Meer, P.J. & Bongers, F. (1996) Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology*, **84**, 19-29.
- van Gelder, H.A., Poorter, L. & Sterck, F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367-378.
- van Gemerden, B.S., Olf, H., Parren, M.P.E., Bongers, F. (2003) The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *Journal of Biogeography*, **30**, 1381-1390.
- van Zon, P. (1915) Mededeelingen omtrent den kamferboom (*Dryobalanops aromatica*). *Tectona*, **8**, 319-324.
- Veenendaal, E.M., Swaine, M.D., Lecha, R.T., Walsh, M.F., Abebrese, I.K. & Owusuafriyie, K. (1996) Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology*, **10**, 501-511.

- Veltman, C.J., Nee, S. & Crawley, M.J. (1996) Correlates of introduction success in exotic New Zealand birds. *American Naturalist*, **147**, 542-557
- Vierling, L.A. & Wessman, C.A. (2000) Photosynthetically active radiation heterogeneity within a monodominant Congolese rain forest canopy. *Agricultural and Forest Meteorology*, **103**, 265-278.
- Vilà, M., Vayreda, J., Comas, L., Ibáñez, J.J., Mata, T. & Obón, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters*, **10**, 241-250.
- Villela, D.M. & Proctor, J. (2002) Leaf litter decomposition and monodominance in the *Peltogyne* forest of Maracá Island, Brazil. *Biotropica*, **34**, 334-347.
- Vitousek, P.M. & Sanford Jr., R.L. (1986). Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137-167.
- Vitousek, P.M. (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forest. *Ecology*, **65**, 285-298.
- Vitousek, P.M. & Sanford, R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137-167.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257-300.
- Walther, B.A. & Morand, S. (1998) Comparative performance of species richness estimation methods. *Parasitology*, **116**, 395-405.
- Wardle, D.A. & Zackrisson, O. (2005) Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806-810.
- Wardle, D.A. (2002) *Communities and Ecosystems: Linking the aboveground and belowground components*. Princeton University Press, Princeton.
- Wardle, DA & Zackrisson, O. (2005) Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806-810.
- Weiher, E., Clarke, G.D.P. & Keddy P.A. (1998) Community assembly rules, morphological

- dispersion, and the coexistence of plant species. *Oikos*, **81**, 309-322.
- Weng, C., Hooghiemstra, H. & Duivenvoorden, J.F. (2006) Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems, and possible solutions. *Diversity and Distributions*, **12**, 310-318.
- Whitmore, T.C. (1984) *Tropical rain forests of the Far East*. (2nd ed.). Clarendon Press, Oxford.
- Whitney, K.D., Fogiel, M.K., Lamperti, A.M., Holbrook, K.M., Stauffer, D.J., Hardesty, B.D., Parker, V.T. & Smith, T.B. (1998) Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, **14**, 351-371.
- Wieder, R.K. & Wright, S.J. (1995) Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology*, **76**, 1971-1979.
- Williams, M.S. & Schreuder, H.T. (2000) Guidelines for choosing volume equations in the presence of measurement error in height. *Canadian Journal of Forest Research*, **30**, 306-310.
- Wills, C., Harms, K.E., Condit, R., King, D., Thompson, J., He, F.L., Muller-Landau, H.C., Ashton, P., Losos, E., Comita, L., Hubbell, S., LaFrankie, J., Bunyavejchewin, S., Dattaraja, H.S., Davies, S., Esufali, S., Foster, R., Gunatilleke, N., Gunatilleke, S., Hall, P., Itoh, A., John, R., Kiratiprayoon, S., de Lao, S.L., Massa, M., Nath, C., Noor, M.N.S., Kassim, A.R., Sukumar, R., Suresh, H.S., Sun, I.F., Tan, S., Yamakura, T. & Zimmerman, E. (2006) Nonrandom processes maintain diversity in tropical forests. *Science*, **311**, 527-531.
- Wilmé, L. (2002) La Reserve de Faune du Dja. ECOFAC, Gabon.
- Wilsey, B.J. & Potvin, C. (2000) Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology*, **81**, 887-892.
- Wittmann, F. & Junk, W.J. (2003) Sapling communities in Amazonian white-water forests. *Journal of Biogeography*, **30**, 1533-1544.
- Worm, B. & Duffy, J.E. (2003) Biodiversity, productivity and stability in real food webs. *Trends in Ecology & Evolution*, **18**, 628-632.

- Wright, S.J. (2005) Tropical forests in a changing environment. *Trends in Ecology and Evolution*, **20**, 553-560.
- Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 1463-1468.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, **424**, 303-306.
- Young, K.D., Ferreira, S.M. & van Aarde, R.J. (2009) The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology*, **34**, 329-342.
- Zalamea, M. & González, G. (2008) Leaf fall phenology in a subtropical wet forest in Puerto Rico: from species to community patterns. *Biotropica*, **40**, 295-304.
- Zedler, J.B., Callaway, J.C. & Sullivan, G. (2001) Declining biodiversity: Why species matter and how their functions might be restored in Californian tidal marshes. *Bioscience*, **51**, 1005-1017.

Appendix A List of tree species and their total number of individuals (dbh >10 cm) found in three 1 ha plots within two forest types, monodominant *Gilbertiodendron* forest (mono) and mixed forest (mix). Occurrence in monodominant forest is indicated by species presence (1) or absence (0). Species in bold had no individual with dbh \geq 10 cm in mixed forest plots.

Family	Name	Occurrence in mono	Forest types	
			mono	mix
Clusiaceae	<i>Allanblackia floribunda</i> Oliv.	0	0	4
Apocynaceae	<i>Alstonia boonei</i> De Wild.	1	1	7
Fabaceae	<i>Amphimas pterocarpoides</i> Harms	0	0	4
Fabaceae	<i>Angylocalyx pynaerthii</i> De Wild.	1	15	6
Annonaceae	<i>Anonidium mannii</i> (Oliv.) Engl. & Diels	1	1	95
Rhizophoraceae	<i>Anopyxis klaineana</i> (Pierre) Engl.	1	1	0
Fabaceae	<i>Anthonotha cladantha</i> (Harms) Léonard	1	1	1
Fabaceae	<i>Anthonotha macrophylla</i> Pal. Beauv.	0	0	9
Eurphorbiaceae	<i>Antidesma</i> sp. A	0	0	1
Sapotaceae	<i>Baillonella toxisperma</i> Pierre	1	2	0
Lauraceae	<i>Beilschmiedia</i> sp. A	0	0	1
Lauraceae	<i>Beilschmiedia</i> sp. B	0	0	1
Sapindaceae	<i>Blighia sapida</i> König	1	3	12
Sapindaceae	<i>Blighia welwitschii</i> (Hiern) Radlk.	1	1	4
Rubiaceae	<i>Brenania brieyi</i> (De Wild.) Petit	0	0	2
Fabaceae	<i>Calpocalyx dinklagei</i> Harms	0	0	1
Burseraceae	<i>Canarium schweinfurthii</i> Engl.	0	0	1
Rubiaceae	<i>Canthium</i> sp. A	0	0	1
Melicaceae	<i>Carapa procera</i> DC.	1	14	66
Melicaceae	<i>Carapa</i> sp. A	0	0	4
Bombaceae	<i>Ceiba pentandra</i> (L.) Gaertn.	0	0	1
Ulmaceae	<i>Celtis tessmannii</i> De Wild.	1	1	15
Ulmaceae	<i>Celtis zenkeri</i> Engl.	1	1	23
Eurphorbiaceae	<i>Centroplocus glaucinus</i> Pierre	1	3	24
Sapindaceae	<i>Chytranthus</i> sp. A	0	0	1
Sapindaceae	<i>Chytranthus</i> sp. B	0	0	1
Sapindaceae	<i>Chytranthus</i> sp. C	0	0	1
Sapindaceae	<i>Chytranthus</i> sp. D	0	0	1
Sapindaceae	<i>Chytranthus</i> sp. E	0	0	1
Sapindaceae	<i>Chytranthus</i> sp. F	0	0	1
Annonaceae	<i>Cleistopholis glauca</i> Pierre ex Engl. & Diels	0	0	5
Annonaceae	<i>Cleistopholis patens</i> (Benth.) Engl. & Diels	0	0	1
Myristicaceae	<i>Coelocaryon preussii</i> Warb.	0	0	6
Rubiaceae	<i>Coffea</i> sp. A	0	0	1
Sterculiaceae	<i>Cola acuminata</i> (P.Beauv.) Schott & Engl.	1	2	6
Sterculiaceae	<i>Cola lateritia</i> K.Schum	0	0	8
Fabaceae	<i>Cylicodiscus gabunensis</i> Harms	0	0	2
Burseraceae	<i>Dacryodes edulis</i> (G.Don) H.J.Lam	0	0	7
Burseraceae	<i>Dacryodes</i> sp. A	0	0	1
Irvingiaceae	<i>Desbordesia glaucescens</i> (Engl.) Van Tiegh.	1	13	13
Tiliaceae	<i>Desplatsia chrysochlamys</i> (Mildbr. & Burrey) Mildbr.	0	0	4
Tiliaceae	<i>Desplatsia dewevrei</i> (De Wild. & Th.Dur.) Burrey	0	0	11
Fabaceae	<i>Dialium guineense</i> Wild.	1	3	5

Family	Name	Occurrence in mono	Forest types	
			mono	mix
Ebenaceae	<i>Diospyros crassiflora</i> Hiern	1	1	4
Ebenaceae	<i>Diospyros hoyleana</i> F.White	0	0	5
Eurphorbiaceae	<i>Discoglypemma caloneura</i> (Pax) Prain	0	0	3
Fabaceae	<i>Distemonanthus benthamianus</i> Baill.	0	0	31
Sapotaceae	<i>Donella pruniformis</i> (Pierre ex Engl.) Aubr. & Pellegr.	0	0	2
Eurphorbiaceae	<i>Drypetes chevalieri</i> Beille	1	1	3
Eurphorbiaceae	<i>Drypetes cf similis</i>	0	0	2
Eurphorbiaceae	<i>Drypetes floribunda</i> (Müll.Arg.) Hutch.	0	0	2
Eurphorbiaceae	<i>Drypetes gossweileri</i> S.Moore	1	1	0
Eurphorbiaceae	<i>Drypetes ivorensis</i> Hutch. & Dalziel	1	2	1
Eurphorbiaceae	<i>Drypetes laciniata</i> (Pax) Hutch.	0	0	3
Eurphorbiaceae	<i>Drypetes</i> sp. A	0	0	1
Eurphorbiaceae	<i>Drypetes</i> sp. B	0	0	1
Eurphorbiaceae	<i>Drypetes</i> sp. C	0	0	1
Eurphorbiaceae	<i>Drypetes</i> sp. D	0	0	1
Eurphorbiaceae	<i>Drypetes</i> sp. E	0	0	1
Eurphorbiaceae	<i>Drypetes</i> sp. F	0	0	1
Tiliaceae	<i>Duboscia macrocarpa</i> Bocq.	1	2	3
Annonaceae	<i>Enantia chlorantha</i> Oliv.	1	1	24
Melicaceae	<i>Entandrophragma angolense</i> (Welw.) C.DC.	0	0	1
Melicaceae	<i>Entandrophragma cylindricum</i> (Sprague) Sprague	1	1	1
Sapindaceae	<i>Eriocoelum macrocarpum</i> Gilg ex Radlk.	1	1	23
Sterculiaceae	<i>Eribroma oblongum</i> (Mast) Pierre ex Germian	0	0	1
Vochysiaceae	<i>Erismadelphus exsul</i> Mildbr.	0	0	1
Fabaceae	<i>Erythrophleum suaveolens</i> (Guil. & Perr.) Brenan	1	1	4
Myrtaceae	<i>Eugenia</i> sp. A	0	0	1
Myrtaceae	<i>Eugenia</i> sp. B	0	0	1
Bigoniaceae	<i>Fernandoa adolfi-frederici</i> Gilg. & Mildbr.	1	1	1
Moraceae	<i>Ficus</i> sp. A	0	0	1
Apocynaceae	<i>Funtumia africana</i> (Benth.) Stapf	0	0	1
Apocynaceae	<i>Funtumia elastica</i> (Preuss) Stapf	0	0	5
Sapotaceae	<i>Gambeya lacourtiana</i> (De Wild.) Aubr.	1	3	10
Sapotaceae	<i>Gambeya perpulchra</i> (Mildbr. Ex Hutch & Dalziel) Aubrév & Pellegr.	0	0	1
Sapotaceae	<i>Gambeya</i> sp. A	0	0	1
Sapotaceae	<i>Gambeya</i> sp. B	0	0	1
Clusiaceae	<i>Garcinia mannii</i> Oliv.	0	0	10
Clusiaceae	<i>Garcinia punctata</i> Stapf	0	0	1
Fabaceae	<i>Gilbertiodendron dewevrei</i> (de Wild.) Léonard	1	805	0
Melicaceae	<i>Guarea cedrata</i> (A.Chev.) Pellegr.	1	1	8
Melicaceae	<i>Guarea thompsonii</i> Sprague & Hutch.	1	1	14
Olacaceae	<i>Heisteria trillesiana</i> Pierre	1	1	18
Olacaceae	<i>Heisteria zimmereri</i> Engl.	0	0	1
Annonaceae	<i>Hexalobus crispiflorus</i> A.Rich.	0	0	3
Flacourtiaceae	<i>Homalium dolichophyllum</i> Gilg	0	0	1
Flacourtiaceae	<i>Homalium letestui</i> Pellegr.	0	0	1
Fabaceae	<i>Hylodendron gabunense</i> Taubert	1	1	6
Eurphorbiaceae	<i>Hymenocardia lyrata</i> Tul.	0	0	4
Eurphorbiaceae	<i>Hymenocardia</i> sp. A	0	0	2
Irvingiaceae	<i>Irvingia gabonensis</i> (Aurey-Lecomte ex O'Rorke) Baill.	1	2	5
Irvingiaceae	<i>Irvingia grandifolia</i> (Engl.) Engl.	1	2	2
Irvingiaceae	<i>Irvingia robur</i> Mildbr.	1	2	1
Fabaceae	<i>Isomacrolobium</i> sp. A	0	0	3

Family	Name	Occurrence	Forest types	
			in mono	mono
Eurphorbiaceae	<i>Keayodendron bridelioides</i> (Hutch. & Dalz.) Léandri	0	0	4
Eurphorbiaceae	<i>Klaineanthus gaboniae</i> Pierre ex Prain	0	0	3
Eurphorbiaceae	<i>Klaineanthus</i> sp. A	0	0	1
Irvingiaceae	<i>Klainedoxa gabonensis</i> Pierre	1	3	7
Anacardiaceae	<i>Lannea welwitschii</i> (Hiern) Engl.	0	0	1
Rhamnaceae	<i>Lasiodiscus mannii</i> Hook.f.	1	1	0
Lepidobotryaceae	<i>Lepidobotrys staudtii</i> Engl.	1	1	12
Chrysobalanaceae	<i>Licania elaeosperma</i> (Mildbr.) Prance & F.White	0	0	1
Melicaceae	<i>Lovoa trichilioides</i> Harms	1	1	3
Eurphorbiaceae	<i>Macaranga</i> sp. A	0	0	3
Eurphorbiaceae	<i>Macaranga spinosa</i> Müll.Arg.	0	0	4
Eurphorbiaceae	<i>Maesobotrya dusenii</i> (Pax) Hutch.	0	0	6
Rhamnaceae	<i>Maesopsis eminii</i> Engl.	0	0	2
Chrysobalanaceae	<i>Magnistipula</i> sp. A	0	0	1
Clusiaceae	<i>Mammea africana</i> Sabine	1	10	1
Sapotaceae	<i>Manilkara letouzeyi</i> Aubr.	0	0	1
Eurphorbiaceae	<i>Mareyopsis longifolia</i> (Pax) Pax & Hoffm.	1	3	0
Chrysobalanaceae	<i>Maranthes glabra</i> (Oliv.) Prance	0	0	2
Chrysobalanaceae	<i>Maranthes</i> sp. A	0	0	1
Eurphorbiaceae	<i>Margaritaria discoidea</i> (Baill.) Webster	0	0	3
Melastomataceae	<i>Memecylon amshoffiae</i> Jacq.-Fél.	0	0	1
Pandaceae	<i>Microdesmis puberula</i> Hook.f. ex Planch.	0	0	2
Moraceae	<i>Milicia excelsa</i> (Welw.) Berg.	0	0	1
Fabaceae	<i>Millettia laurentii</i> De Wild.	0	0	1
Moraceae	<i>Musanga cecropioides</i> R.Br.	0	0	1
Moraceae	<i>Myrianthus arboreus</i> P.Beauv.	0	0	21
Rubiaceae	<i>Nauclea diderrichii</i> (De Wild.) Merrill	0	0	3
Simaroubaceae	<i>Odyendya gabonensis</i> (Pierre) Engl.	1	5	2
Flacourtiaceae	<i>Oncoba glauca</i> (P.Beauv.) Planch.	0	0	29
Olaceae	<i>Ongokea gore</i> Pierre	1	3	2
Annonaceae	<i>Pachypodanthium staudtii</i> (Engl. & Diels)	0	0	3
Sapindaceae	<i>Pancovia pedicellaris</i> Radlk. & Gilg.	0	0	1
Pandaceae	<i>Panda oleosa</i> Pierre	1	1	15
Fabaceae	<i>Parkia bicolor</i> A.Chev.	0	0	5
Rubiaceae	<i>Pauridiantha floribunda</i> (K.Schum. Ex K.Krause) Bremek.	0	0	2
Rubiaceae	<i>Pausinystalia macroceras</i> (K.Schum.) Pierre	0	0	1
Fabaceae	<i>Pentaclethra macrophylla</i> Benth.	1	11	45
Lecythidaceae	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	1	1	60
Apocynaceae	<i>Picalima nitida</i> (Stapf) Th.Dur.	0	0	3
Mimosaceae	<i>Piptadeniastrum africanum</i> (Hook.f.) Brenan	0	0	6
Eurphorbiaceae	<i>Plagiostyles africana</i> (Müll.Arg.) Prain	1	1	0
Annonaceae	<i>Polyalthia suaveolens</i> Engl. & Diels	1	7	67
Anacardiaceae	<i>Pseudospondias microcarpa</i> (A.Rich.) Engl.	0	0	4
Combretaceae	<i>Pteleopsis hylodendron</i> Mildbr.	0	0	1
Fabaceae	<i>Pterocarpus müldbraedii</i> Harms	0	0	4
Fabaceae	<i>Pterocarpus soyauxii</i> Taub.	1	2	11
Myristicaceae	<i>Pycnanthus angolensis</i> (Welw.) Exell	0	0	5
Apocynaceae	<i>Rauvolfia vomitoria</i> Afz.	0	0	3
Ochnaceae	<i>Rhabdophyllum</i> sp. A	0	0	1
Ochnaceae	<i>Rhabdophyllum</i> sp. B	0	0	1
Ochnaceae	<i>Rhabdophyllum</i> sp. C	0	0	2
Ochnaceae	<i>Rhabdophyllum</i> sp. D	1	1	0

Family	Name	Occurrence in mono	Forest types	
			mono	mix
Violaceae	<i>Rinorea oblongifolia</i> (C.H.Wright) Marquand ex Chipp	0	0	3
Violaceae	<i>Rinorea welwitschii</i> (Oliv.) Kuntze	0	0	1
Violaceae	<i>Rinorea</i> sp. A	1	1	0
Rubiaceae	<i>Rothmannia lujae</i> (De Wild.) Keay	1	2	20
Burseraceae	<i>Santiria trimera</i> (Oliv.) Aubrév.	1	7	30
Flacourtiaceae	<i>Scottellia</i> sp. A	0	0	1
Anacardiaceae	<i>Sorindeia grandifolia</i> Engl.	1	3	18
Anacardiaceae	<i>Sorindeia mildbraedii</i> Engl. & Brehmer	1	2	12
Myristicaceae	<i>Staudtia stipitata</i> Warb.	1	12	8
Sterculiaceae	<i>Sterculia tragacantha</i> Lindl.	0	0	1
Olacaceae	<i>Strombosia grandifolia</i> Hook.f.	1	5	5
Olacaceae	<i>Strombosia pustulata</i> Oliv.	1	11	3
Olacaceae	<i>Strombosia zenkeri</i> Engl.	0	0	1
Olacaceae	<i>Strombosiopsis tetrandra</i> Engl.	1	3	8
Clusiaceae	<i>Symphonia globulifera</i> L.F.	0	0	2
Sapotaceae	<i>Synsepalum dulcificum</i> (Schum.) Baill.	1	1	11
Myrtaceae	<i>Syzygium rowlandii</i> (Engl.) Mildbr.	0	0	4
Apocynaceae	<i>Tabernaemontana crassa</i> Benth.	1	2	54
Fabaceae	<i>Tessmannia africana</i> Harms	1	2	1
Fabaceae	<i>Tessmannia anomala</i> (Micheli) Harms	1	4	0
Fabaceae	<i>Tetrapleura tetraptera</i> (Schum. & Thonn.) Taub.	0	0	3
Moraceae	<i>Treculia africana</i> Desc.	1	3	1
Rubiaceae	<i>Tricalysia discolor</i> Brenan	0	0	2
Rubiaceae	<i>Tricalysia</i> sp. A	0	0	1
Rubiaceae	<i>Tricalysia</i> sp. B	0	0	1
Melicaceae	<i>Trichilia prieuriana</i> A.Juss.	0	0	1
Melicaceae	<i>Trichilia rubescens</i> Oliv.	0	0	12
Melicaceae	<i>Trichilia welwitschii</i> C.DC.	1	1	3
Anacardiaceae	<i>Trichoscypha acuminata</i> Engl.	1	11	22
Anacardiaceae	<i>Trichoscypha arborea</i> (A.Chev.) A.Chev.	0	0	1
Sapotaceae	<i>Tridesmostemon omphalocarpoides</i> Engl.	0	0	2
Moraceae	<i>Trilepisium madagascariense</i> DC.	0	0	1
Eurphorbiaceae	<i>Uapaca acuminata</i> (Hutch.) Pax & Hoffm.	1	1	20
Eurphorbiaceae	<i>Uapaca guineensis</i> Müll.Argr.	0	0	23
Eurphorbiaceae	<i>Uapaca paluosa</i> Aubrév. & Léandri	0	0	34
Eurphorbiaceae	<i>Uapaca vanhoutei</i> De Wild.	0	0	2
Verbenaceae	<i>Vitex cienkowskii</i> Kotschy & Peyr.	0	0	9
Verbenaceae	<i>Vitex grandifolia</i> Gürke	0	0	1
Annonaceae	<i>Xylopi aethiopica</i> (Dun.) A.Rich.	0	0	2
Annonaceae	<i>Xylopi hypolampra</i> Mildbr.	1	1	3
Annonaceae	<i>Xylopi parviflora</i> (A.Rich.) Benth.	1	1	0
Annonaceae	<i>Xylopi quintasii</i> Engl. & Diels	1	1	14
Annonaceae	<i>Xylopi staudtii</i> Engl. & Diels	0	0	1
Annonaceae	<i>Xylopi</i> sp. A	0	0	1
Annonaceae	<i>Xylopi</i> sp. B	0	0	1
Rutaceae	<i>Zanthoxylum gillettii</i> (De Wild.) Waterman	0	0	2
Rutaceae	<i>Zanthoxylum heitzii</i> (Aubr. & Pellegr.) Waterman	0	0	1
	Unidentified sp. A	0	0	1
	Unidentified sp. B	0	0	1
	Unidentified sp. C	0	0	1
	Unidentified sp. D	0	0	1
	Unidentified sp. E	0	0	1

Family	Name	Occurrence in mono	Forest types	
			mono	mix
	Unidentified sp. F	0	0	1
	Unidentified sp. G	0	0	1
	Unidentified sp. H	0	0	1
	Unidentified sp. I	0	0	1
	Unidentified sp. J	0	0	1
	Unidentified sp. K	0	0	1
	Unidentified sp. L	0	0	1
	Unidentified sp. M	0	0	1
	Unidentified sp. N	0	0	1
	Unidentified sp. O	0	0	1
	Unidentified sp. P	1	1	0
	Unidentified sp. Q	1	1	0

Appendix B Life-history trait data set for the 193 species at the Dja Faunal Reserve based on published literature (e.g., Sonké 2004). The relative abundance of each species in the mixed forests was based on the three mixed forest plots. Wood mass density is defined as dry wood mass/green wood volume (g cm^{-3}) and is compiled from Lewis *et al.* (2009). Species were classified according to maximum stature in three classes: large trees (>30 m tall), medium trees (10–30 m tall) and small trees (<10 m tall). Species were placed on the basis of maximum dbh in three classes: large diameter (>100 cm in dbh), medium diameter (50 cm–100 cm) and small diameter (<50 cm). Each species is classified in one of two categories according to its fruit/seed dispersal mode (biotic and non-biotic dependent). Each species was classified into one of two categories according to its ecological guild in terms of light requirement (pioneer [e.g., light-demanders that require high light level for seedling establishment], and non-pioneer [shade-bearers that are capable of seedling establishment under forest shade, though some shade-bears may need higher light level at later stage of life]), and each was grouped according to its geographical distribution (narrow, i.e., species endemic to lower-Guinea-Congolean biogeographical region; and wide that includes species which were not endemic to the region).

Species name	Family	Presence	Relative abundance	Wood mass density (g cm^{-3})	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Allanblackia floribunda</i>	Clusiaceae	0	4	0.723	large	medium	biotic	pioneer	narrow
<i>Alstonia boonei</i>	Apocynaceae	1	7	0.323	large	large	non-biotic	pioneer	narrow
<i>Amphirmas pterocarpoides</i>	Caesalpiniaceae	0	4	0.565	large	large	non-biotic	non-pioneer	narrow
<i>Angylocalyx pynaerthii</i>	Fabaceae	1	6	0.655	small	small	biotic	non-pioneer	narrow
<i>Anonidium mannii</i>	Annonaceae	1	95	0.293	medium	medium	biotic	non-pioneer	narrow
<i>Anopyxis klaineana</i>	Anisophylleaceae	1	0	0.811	large	large	biotic	non-pioneer	narrow
<i>Anthonotha cladantha</i>	Caesalpiniaceae	1	1	0.577	medium	medium	non-biotic	non-pioneer	narrow
<i>Anthonotha macrophylla</i>	Caesalpiniaceae	0	9	0.849	medium	small	non-biotic	non-pioneer	narrow
<i>Antidesma sp. A</i>	Eurphorbiaceae	0	1	0.613					
<i>Baillonella toxisperma</i>	Sapotaceae	1	0	0.729	large	large	biotic	non-pioneer	narrow
<i>Beilschmiedia sp. A</i>	Lauraceae	0	1	0.637					
<i>Beilschmiedia sp. B</i>	Lauraceae	0	1	0.637					
<i>Blighia sapida</i>	Sapindaceae	1	12	0.784	medium	medium	biotic	non-pioneer	narrow
<i>Blighia welwitschii</i>	Sapindaceae	1	4	0.820	large	large	biotic	non-pioneer	narrow
<i>Brenania brieyi</i>	Rubiaceae	0	2	0.541	large	medium	biotic	non-pioneer	narrow
<i>Calpocalyx dinklagei</i>	Mimosaceae	0	1	0.648	small	small	biotic	non-pioneer	narrow

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Canarium schweinfurthii</i>	Burseraceae	0	1	0.414	large	large	biotic	non-pioneer	narrow
<i>Canthium sp. A</i>	Rubiaceae	0	1	0.661					
<i>Carapa procera</i>	Melicaceae	1	66	0.630	large	large	biotic	non-pioneer	wide
<i>Carapa sp. A</i>	Melicaceae	0	4	0.555					
<i>Ceiba pentandra</i>	Bombaceae	0	1	0.277	large	large	non-biotic	pioneer	wide
<i>Celtis tessmannii</i>	Ulmaceae	1	15	0.656	large	large	biotic	non-pioneer	narrow
<i>Celtis zenkeri</i>	Ulmaceae	1	23	0.620	large	large	biotic	non-pioneer	narrow
<i>Centropachus glaucinus</i>	Eurphorbiaceae	1	24	0.523	small	small	biotic	non-pioneer	narrow
<i>Chytranthus sp. A</i>	Sapindaceae	0	1	0.593					
<i>Chytranthus sp. B</i>	Sapindaceae	0	1	0.593					
<i>Chytranthus sp. C</i>	Sapindaceae	0	1	0.593					
<i>Chytranthus sp. D</i>	Sapindaceae	0	1	0.593					
<i>Chytranthus sp. E</i>	Sapindaceae	0	1	0.593					
<i>Chytranthus sp. F</i>	Sapindaceae	0	1	0.593					
<i>Cleistopholis glauca</i>	Annonaceae	0	5	0.309	medium	small	biotic	non-pioneer	narrow
<i>Cleistopholis patens</i>	Annonaceae	0	1	0.348	medium	medium	biotic	non-pioneer	narrow
<i>Coelocaryon preussii</i>	Myristicaceae	0	6	0.499	medium	medium	biotic	non-pioneer	narrow
<i>Coffea sp. A</i>	Rubiaceae	0	1	0.541					
<i>Cola acuminata</i>	Sterculiaceae	1	6	0.556	medium	small	biotic	non-pioneer	narrow
<i>Cola lateritia</i>	Sterculiaceae	0	8	0.590	large	medium	biotic	non-pioneer	narrow
<i>Cylicodiscus gabonensis</i>	Mimosaceae	0	2	0.799	large	large	non-biotic	non-pioneer	narrow
<i>Dacryodes edulis</i>	Burseraceae	0	7	0.528	medium	medium	biotic	pioneer	narrow
<i>Dacryodes sp. A</i>	Burseraceae	0	1	0.554					
<i>Desbordesia glaucescens</i>	Irvingiaceae	1	13	0.921	large	large	non-biotic	non-pioneer	narrow
<i>Desplatsia chrysochlamys</i>	Tiliaceae	0	4	0.561	small	small	biotic	non-pioneer	narrow
<i>Desplatsia dewevrei</i>	Tiliaceae	0	11	0.561	small	small	biotic	non-pioneer	narrow
<i>Dialium guineensis</i>	Caesalpiniaceae	1	5	0.885	medium	medium	non-biotic	non-pioneer	narrow
<i>Diospyros crassifolia</i>	Ebenaceae	1	4	0.881	medium	large	biotic	non-pioneer	narrow
<i>Diospyros hoyleana</i>	Ebenaceae	0	5	0.826	small	small	biotic	non-pioneer	narrow
<i>Discoglyprena caloneura</i>	Eurphorbiaceae	0	3	0.351	medium	medium	biotic	pioneer	narrow

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Distemonanthus benthamianus</i>	Caesalpiniaceae	0	31	0.575	large	large	non-biotic	non-pioneer	narrow
<i>Donella pruniformis</i>	Sapotaceae	0	2	0.635	large	medium	biotic	non-pioneer	narrow
<i>Drypetes cf similis</i>	Eurphorbiaceae	0	2	0.671					
<i>Drypetes chevalieri</i>	Eurphorbiaceae	1	3	0.630	small	small	biotic	non-pioneer	narrow
<i>Drypetes floribunda</i>	Eurphorbiaceae	0	2	0.671	small				
<i>Drypetes goosweleiri</i>	Eurphorbiaceae	1	0	0.672	large	small	biotic	non-pioneer	narrow
<i>Drypetes ivorensis</i>	Eurphorbiaceae	1	1	0.671	large	small	biotic	non-pioneer	narrow
<i>Drypetes laciniata</i>	Eurphorbiaceae	0	3	0.630	small	small	biotic	non-pioneer	narrow
<i>Drypetes</i> sp. A	Eurphorbiaceae	0	1	0.671					
<i>Drypetes</i> sp. B	Eurphorbiaceae	0	1	0.671					
<i>Drypetes</i> sp. C	Eurphorbiaceae	0	1	0.671					
<i>Drypetes</i> sp. D	Eurphorbiaceae	0	1	0.671					
<i>Drypetes</i> sp. E	Eurphorbiaceae	0	1	0.671					
<i>Drypetes</i> sp. F	Eurphorbiaceae	0	1	0.671					
<i>Duboscia macrocarpa</i>	Tiliaceae	1	3	0.561	large	large	biotic	non-pioneer	narrow
<i>Enantia chlorantha</i>	Annonaceae	1	24	0.424	medium	small	biotic	non-pioneer	narrow
<i>Entandrophragma angolense</i>	Melicaceae	0	1	0.497	large	large	non-biotic	non-pioneer	narrow
<i>Entandrophragma cylindricum</i>	Melicaceae	1	1	0.577	large	large	non-biotic	non-pioneer	narrow
<i>Eribroma oblongum</i>	Sterculiaceae	0	1	0.590	large	large	biotic	non-pioneer	narrow
<i>Eriocoelum macrocarpum</i>	Sapindaceae	1	23	0.500	medium	medium	non-biotic	non-pioneer	narrow
<i>Erismadelphus exul</i>	Vochysiaceae	0	1	0.608	large	large	non-biotic	non-pioneer	narrow
<i>Erythrophloeum suaveolens</i>	Caesalpiniaceae	1	4	0.842	large	large	non-biotic	non-pioneer	wide
<i>Eugenia</i> sp. B	Myrtaceae	0	1	0.613					
<i>Eugenia</i> sp. A	Myrtaceae	0	1	0.613					
<i>Fernandoa adolphi-frederici</i>	Bigononiaceae	1	1	0.589	medium	medium	non-biotic	pioneer	narrow
<i>Ficus</i> sp. A	Moraceae	0	1	0.540					
<i>Funtumia africana</i>	Apocynaceae	0	1	0.449	medium	small	non-biotic	pioneer	narrow
<i>Funtumia elastica</i>	Apocynaceae	0	5	0.425	medium	small	non-biotic	pioneer	narrow
<i>Gambeya lacourtiana</i>	Sapotaceae	1	10	0.611	large	large	biotic	non-pioneer	narrow
<i>Gambeya perpulchra</i>	Sapotaceae	0	1	0.595					

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Gambeya</i> sp. A	Sapotaceae	0	1	0.595					
<i>Gambeya</i> sp. B	Sapotaceae	0	1	0.595					
<i>Garcinia mannii</i>	Clusiaceae	0	10	0.835	medium	small	biotic	non-pioneer	narrow
<i>Garcinia punctata</i>	Clusiaceae	0	1	0.835	large	small	biotic	non-pioneer	narrow
<i>Guarea cedrata</i>	Melicaceae	1	8	0.516	large	large	biotic	non-pioneer	narrow
<i>Guarea thompsonii</i>	Melicaceae	1	14	0.563	large	large	biotic	non-pioneer	narrow
<i>Heisteria trillesiana</i>	Olacaceae	1	18	0.734	medium	large	biotic	non-pioneer	narrow
<i>Heisteria zimmereri</i>	Olacaceae	0	1	0.734	large	large	biotic	non-pioneer	narrow
<i>Hexalobus crispiliformis</i>	Annonaceae	0	3	0.486	medium	large	biotic	non-pioneer	narrow
<i>Homalium dolichophyllum</i>	Flacourtiaceae	0	1	0.737	medium	large	biotic	non-pioneer	narrow
<i>Homalium letestui</i>	Flacourtiaceae	0	1	0.725	medium	small	biotic	non-pioneer	narrow
<i>Hylocodendron gabunense</i>	Caesalpiniaceae	1	6	0.792	medium	large	non-biotic	non-pioneer	narrow
<i>Hymenocardia lyrata</i>	Eurphorbiaceae	0	4	0.523	medium	medium	non-biotic	pioneer	narrow
<i>Hymenocardia</i> sp. A	Eurphorbiaceae	0	2	0.523					
<i>Irvingia gabonensis</i>	Irvingiaceae	1	5	0.794	medium	large	biotic	non-pioneer	narrow
<i>Irvingia grandifolia</i>	Irvingiaceae	1	2	0.803	large	large	biotic	non-pioneer	narrow
<i>Irvingia robur</i>	Irvingiaceae	1	1	0.707	large	large	biotic	non-pioneer	narrow
<i>Isomacrolobium</i> sp. A	Fabaceae	0	3	0.655					
<i>Keayodendron bridelioides</i>	Eurphorbiaceae	0	4	0.523	medium	medium	biotic	non-pioneer	narrow
<i>Klaineanthus gabonae</i>	Eurphorbiaceae	0	3	0.523	medium	small	biotic	non-pioneer	narrow
<i>Klaineanthus</i> sp. A	Eurphorbiaceae	0	1	0.523					
<i>Klainedoxa gabonensis</i>	Irvingiaceae	1	7	0.940	large	large	biotic	non-pioneer	narrow
<i>Lannea welwitschii</i>	Anacardiaceae	0	1	0.425	large	large	biotic	non-pioneer	narrow
<i>Lasiodiscus mannii</i>	Rhamnaceae	1	0	0.379	small	small	biotic	non-pioneer	narrow
<i>Lepidobotrys staudtii</i>	Lepidobotryaceae	1	12		medium	medium	biotic	non-pioneer	narrow
<i>Licania elaeosperma</i>	Chrysobalanaceae	0	1	0.702					
<i>Lovoa trichiloides</i>	Melicaceae	1	3	0.460	large	large	non-biotic	non-pioneer	narrow
<i>Macaranga grandis</i>	Eurphorbiaceae	0	3	0.394	medium	small	biotic	pioneer	narrow
<i>Macaranga spinosa</i>	Eurphorbiaceae	0	4	0.394	medium	small	biotic	pioneer	narrow
<i>Maesobotrya dusenii</i>	Eurphorbiaceae	0	6	0.525					

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Maesopsis eminii</i>	Rhamnaceae	0	2	0.396	large	medium	biotic	pioneer	narrow
<i>Magnistipula</i> sp. A	Clusiaceae	0	1	0.702					
<i>Mammea africana</i>	Clusiaceae	1	1	0.633	large	large	biotic	non-pioneer	narrow
<i>Manilkara letouzeyi</i>	Sapotaceae	0	1	0.828	large	large	biotic	non-pioneer	narrow
<i>Maranthes glabra</i>	Chrysobalanaceae	0	2	0.881	large	large	biotic	non-pioneer	narrow
<i>Maranthes</i> sp. A	Chrysobalanaceae	0	1	0.702					
<i>Mareyopsis longifolia</i>	Eurphorbiaceae	1	0	0.523	small	small	biotic	non-pioneer	narrow
<i>Margaritaria discoidea</i>	Eurphorbiaceae	0	3	0.776	large	large	biotic	pioneer	wide
<i>Memecylon amshoffiae</i>	Melastomataceae	0	1	0.824	small	small			
<i>Microdesmis puberula</i>	Pandaceae	0	2		small	small	biotic	non-pioneer	narrow
<i>Milicia exelsa</i>	Moraceae	0	1	0.575	large	large	biotic	pioneer	narrow
<i>Millettia laurentii</i>	Fabaceae	0	1	0.764	medium	small	non-biotic	non-pioneer	narrow
<i>Musanga cecropioides</i>	Moraceae	0	1	0.247	medium	large	biotic	pioneer	narrow
<i>Myrianthus arboreus</i>	Moraceae	0	21	0.454	medium	small	biotic	pioneer	narrow
<i>Nauclea diderrichii</i>	Rubiaceae	0	3	0.673	large	medium	biotic	pioneer	narrow
<i>Odyendya gabonensis</i>	Simaroubaceae	1	2	0.327	medium	large	biotic	non-pioneer	narrow
<i>Oncoba glauca</i>	Flacourtiaceae	0	29	0.652	medium	small			
<i>Ongoeka gore</i>	Olacaceae	1	2	0.769	large	large	biotic	non-pioneer	narrow
<i>Pachypodanthium staudtii</i>	Annonaceae	0	3	0.580	medium	medium	biotic	non-pioneer	narrow
<i>Pancovia pedicellaris</i>	Sapindaceae	0	1	0.635	medium	small	biotic	non-pioneer	narrow
<i>Panda oleosa</i>	Pandaceae	1	15		large	medium	biotic	non-pioneer	narrow
<i>Parkia bicolor</i>	Mimosaceae	0	5	0.469	large	large	biotic	non-pioneer	narrow
<i>Pauridiantha floribunda</i>	Rubiaceae	0	2	0.541	small	small	biotic	pioneer	narrow
<i>Pausynistalia macroceras</i>	Rubiaceae	0	1	0.560	medium	small	biotic	non-pioneer	narrow
<i>Pentaclethra macrophylla</i>	Mimosaceae	1	45	0.867	medium	large	non-biotic	non-pioneer	narrow
<i>Petersianthus macrocarpus</i>	Lecythidaceae	1	60	0.690	large	large	non-biotic	non-pioneer	narrow
<i>Picalima nitida</i>	Apocynaceae	0	3	0.785	medium	small	biotic	non-pioneer	narrow
<i>Piptadeniastrum africana</i>	Mimosaceae	0	6	0.613	large	large	non-biotic	non-pioneer	narrow
<i>Plagiostyles africana</i>	Eurphorbiaceae	1	0	0.748	medium	small	biotic	non-pioneer	narrow
<i>Polyalthia suaveolens</i>	Annonaceae	1	67	0.704	medium	small	biotic	non-pioneer	narrow

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Pseudospondias microcarpa</i>	Anacardiaceae	0	4	0.461	medium	medium	biotic	non-pioneer	wide
<i>Pteleopsis hylodendron</i>	Combretaceae	0	1	0.681	large	large	non-biotic	non-pioneer	narrow
<i>Pterocarpus mildbreadii</i>	Fabaceae	0	4	0.589	large	large	non-biotic	non-pioneer	narrow
<i>Pterocarpus soyauxii</i>	Fabaceae	1	11	0.661	large	large	non-biotic	non-pioneer	narrow
<i>Pycnanthus angolensis</i>	Myristicaceae	0	5	0.414	large	large	biotic	pioneer	narrow
<i>Rauvolfia vomitoria</i>	Apocynaceae	0	3	0.484	small	small	biotic	pioneer	narrow
<i>Rhabdophyllum</i> sp. A	Ochnaceae	0	1	0.752					
<i>Rhabdophyllum</i> sp. B	Ochnaceae	0	1	0.752					
<i>Rhabdophyllum</i> sp. C	Ochnaceae	0	2	0.752					
<i>Rhabdophyllum</i> sp. D	Ochnaceae	1	0	0.752					
<i>Rinorea oblongifolia</i>	Violaceae	0	3		small	small	biotic	non-pioneer	narrow
<i>Rinorea</i> sp. A	Violaceae	1	0						
<i>Rinorea welwitschii</i>	Violaceae	0	1		small	small	biotic	non-pioneer	narrow
<i>Rothmannia lujae</i>	Rubiaceae	1	20	0.541	medium	small	biotic	non-pioneer	narrow
<i>Santiria trimera</i>	Burseraceae	1	30	0.549	medium	medium	biotic	non-pioneer	narrow
<i>Scottellia</i> sp. A	Flacourtiaceae	0	1	0.549					
<i>Sorindeia grandifolia</i>	Anacardiaceae	1	18	0.560	medium	small	biotic	non-pioneer	narrow
<i>Sorindeia mildbraedii</i>	Anacardiaceae	1	12	0.560	medium	small	biotic	non-pioneer	narrow
<i>Staudtia stipitata</i>	Myristicaceae	1	8	0.723	medium	large	biotic	non-pioneer	narrow
<i>Sterculia tragacantha</i>	Sterculiaceae	0	1	0.641	medium	medium	biotic	pioneer	wide
<i>Strombosia grandifolia</i>	Olacaceae	1	5	0.843	medium	small	biotic	non-pioneer	narrow
<i>Strombosia pustulata</i>	Olacaceae	1	3	0.854	medium	small	biotic	non-pioneer	narrow
<i>Strombosia zenkeri</i>	Olacaceae	0	1	0.777	medium	medium	biotic	non-pioneer	narrow
<i>Strombosiopsis tetandra</i>	Olacaceae	1	8	0.671	medium	large	biotic	non-pioneer	narrow
<i>Symphonia globulifera</i>	Clusiaceae	0	2	0.601	large	large	biotic	non-pioneer	wide
<i>Synsepalum dulcificum</i>	Sapotaceae	1	11	0.678	medium	small	biotic	non-pioneer	narrow
<i>Syzygium rowlandii</i>	Myrtaceae	0	4	0.611	medium	medium	biotic	non-pioneer	narrow
<i>Tabernaemontana crassa</i>	Apocynaceae	1	54	0.640	medium	small	biotic	pioneer	narrow
<i>Tessmannia africana</i>	Caesalpiniaceae	1	1	0.835	large	large	non-biotic	non-pioneer	narrow
<i>Tessmannia anomala</i>	Caesalpiniaceae	1	0	0.797					

Species name	Family	Presence	Relative abundance	Wood mass density (g cm ⁻³)	Maximum height	Diameter at breast height	Dispersal mechanism	Light requirement	Geographical distribution
<i>Tetrapleura tetraptera</i>	Mimosaceae	0	3	0.588	medium	medium	non-biotic	non-pioneer	narrow
<i>Treculia africana</i>	Moraceae	1	1	0.454	medium	medium	biotic	non-pioneer	wide
<i>Tricalysia discolor</i>	Rubiaceae	0	2	0.541	medium	small	biotic	non-pioneer	narrow
<i>Tricalysia</i> sp. A	Rubiaceae	0	1	0.541					
<i>Tricalysia</i> sp. B	Rubiaceae	0	1	0.541					
<i>Trichilia prieuriana</i>	Melicaceae	0	1	0.671	medium	small	biotic	non-pioneer	narrow
<i>Trichilia rubescens</i>	Melicaceae	0	12	0.565	medium	large	biotic	non-pioneer	narrow
<i>Trichilia welwitschii</i>	Melicaceae	1	3	0.565	medium	medium	biotic	non-pioneer	narrow
<i>Trichoscypha acuminata</i>	Anacardiaceae	1	22	0.615	small	small	biotic	non-pioneer	narrow
<i>Trichoscypha arborea</i>	Anacardiaceae	0	1	0.670	large	large	biotic	non-pioneer	narrow
<i>Tridesmostemon omphalocarpoides</i>	Sapotaceae	0	2	0.635	large	large	biotic	non-pioneer	narrow
<i>Trilepisium madascariensis</i>	Moraceae	0	1	0.454	medium	medium	biotic	non-pioneer	narrow
<i>Uapaca acuminata</i>	Eurphorbiaceae	1	20	0.613	medium	large	biotic	non-pioneer	narrow
<i>Uapaca guineensis</i>	Eurphorbiaceae	0	23	0.642	medium	medium	biotic	non-pioneer	narrow
<i>Uapaca paluosa</i>	Eurphorbiaceae	0	34	0.705	large	large	biotic	non-pioneer	narrow
<i>Uapaca vanhoutei</i>	Eurphorbiaceae	0	2	0.613	medium	small	biotic	non-pioneer	narrow
<i>Vitex cienkowskii</i>	Verbenaceae	0	9	0.532					
<i>Vitex grandifolia</i>	Verbenaceae	0	1	0.532	medium	medium	biotic	non-pioneer	narrow
<i>Xylopiya aethiopica</i>	Annonaceae	0	2	0.475	large	medium	biotic	non-pioneer	narrow
<i>Xylopiya hypolampra</i>	Annonaceae	1	3	0.643	medium	medium	biotic	non-pioneer	narrow
<i>Xylopiya paviflora</i>	Annonaceae	1	0	0.810	medium	large	biotic	non-pioneer	narrow
<i>Xylopiya quintasii</i>	Annonaceae	1	14	0.804	medium	medium	biotic	non-pioneer	narrow
<i>Xylopiya</i> sp. A	Annonaceae	0	1	0.653					
<i>Xylopiya</i> sp. B	Annonaceae	0	1	0.653					
<i>Xylopiya staudtii</i>	Annonaceae	0	1	0.439	medium			non-pioneer	
<i>Zanthoxylum giletii</i>	Rutaceae	0	2	0.705	medium	large	biotic	non-pioneer	narrow
<i>Zanthoxylum hetzii</i>	Rutaceae	0	1	0.451	medium	large	biotic	non-pioneer	narrow