Secondary Succession in Tropical Dry Forests

Drivers and Mechanisms of Forest Regeneration

Géraldine Derroire

Bangor University
College of Natural Sciences
School of Environment, Natural Resources and Geography
&
Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Southern Swedish Forest Research Centre, Alnarp

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Cover: Tropical dry forest of Santa Rosa, Costa Rica
 (photo: Géraldine Derroire)

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Abstract

Secondary succession is a complex process involving numerous factors acting across scales. Understanding secondary succession in tropical dry forests is important for the conservation and restoration of this highly threatened biome. My research aims to improve knowledge of the trajectories and drivers of secondary succession in this biome, and the underlying mechanisms. I used a combination of literature synthesis, observational and experimental approaches to study plant-plant interactions and community changes during succession.

  Through review of published studies, I showed that established trees have a mainly positive effect on the seed dispersal, survival and germination of the subsequent generation of woody plants. However, the balance between positive and negative effects is more complex at the seedling establishment stage and can be influenced by the precipitation regime. Meta-analyses of chronosequence studies showed an increase in tree and shrub species richness with succession and a slow convergence of successional forest species composition with that of old-growth forests. Using survey of young woody plants establishing under isolated trees in pastures, I showed that the attributes of the trees influence the functional composition of the regeneration assemblages but are only weakly related to their taxonomic composition. The position of isolated trees in the landscape is also influential, but this is complex and site-specific. Through extensive sampling of leaf functional traits of sapling communities in secondary forests of different successional age, I found that community functional composition shifts from conservative towards acquisitive strategies of resource economics, through both species turnover and intraspecific variation of trait values. Five of the measured traits also showed directional changes with tree ontogeny. Lastly, an experimental test of seed fate showed that leaf litter reduced seed removal in successional forests. Seed germination rate was higher in successional forests compared with open sites and generally benefited from the presence of litter. Overall, this research suggests a higher predictability of successional trajectories when studied through functional rather than taxonomic composition. It also shows heterogeneity in successional trajectories among tropical dry forests that require further study.

Keywords: biodiversity, community assembly, Costa Rica, environmental gradients, facilitation, plant functional traits, regeneration niche

Author's address: Géraldine Derroire, Bangor University, School of Environment, Natural Resources and Geography, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK
E-mail: g.derroire@bangor.ac.uk

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I   Derroire, G., Tigabu, M., Odén P.C., Healey, J.H. (2016). The effects of established trees on woody regeneration during secondary succession in tropical dry forests. *Biotropica,* 48(3), pp. 290-300.

II Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E., Leiva, J.A. , Odén, P.C., Powers, J.S., Rico-Gray, V., Tigabu, M., Healey J.R. (2016). Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos,* doi: 10.1111/oik.03229.

III Derroire, G., Coe, R., Healey, J.H. (2016). Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors. *Journal of Vegetation Science*, doi:10.1111/jvs.12404.

IV Derroire, G., Powers, J.S., Hulshof, C.M., Cárdenas Valera, L.E, Healey, J.H. Functional strategies change through species turnover and intraspecific variation in tropical dry forest succession (manuscript under review).

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Preliminary results of a study of the influence of changing abiotic and biotic environmental conditions during succession on the fate of seeds (referred to as the study of seed fate) are also presented and discussed in the thesis.

The contribution of Géraldine Derroire (GD) to the papers included in this thesis was as follows:

I   GD reviewed the literature, carried out the analysis and wrote the first version of the paper. All co-authors contributed to editing the paper. GD was responsible for most of the correspondence with the journal, with advice from John Healey (JH). The overall contribution of GD is estimated to be 95%.

II GD designed this study with advice from JH, reviewed the literature, corresponded with authors of published papers to obtain data, carried out the meta-analysis and wrote the first version of the paper. All co-authors contributed to editing the paper. GD was responsible for most of the correspondence with the journal, with advice from JH and input from co-authors. The overall contribution of GD is estimated to be 95%.

III GD designed this study with advice from JH and collected the data with Roberto Espinoza. GD did the statistical analysis with advice from Richard Coe. GD wrote the first version of the paper and all co-authors edited it. GD was responsible for most of the correspondence with the journal, with advice from JH. The overall contribution of GD is estimated to be 95%.

IV GD designed the study with advice from JH, Jennifer Powers and Catherine Hulshof. GD was responsible for data collection with help from Luis Cárdenas Valera, Daniel Perez Aviles, Christina Smith and Erick Calderon Morales. GD carried out the chemical analyses and the statistical analysis. GD wrote the first version of the paper and all co-authors edited it. The overall contribution of GD is estimated to be 95%.

Abbreviations

ACG	*Área de Conservación de Guanacaste*
AIC	Akaike information criterion
ANOVA	Analysis of variance
DBH	Diameter at breast height
FAO	Food and agriculture organisation
FRA	Global forest resources assessment
GLM	Generalised linear model
LA	Leaf area
LCC	Leaf carbon concentration
LDMC	Leaf dry matter content
LNC	Leaf nitrogen concentration
LPC	Leaf phosphorous concentration
PCA	Principal component analysis
PIC	Phylogenetically independent contrast
RDA	Redundancy analysis
SLA	Specific leaf area

1 Introduction

1.1 Importance of tropical secondary forests

Most of the tropical forests of the future are expected to be "secondary forests regenerating after previous clearing" (Wright & Muller-Landau, 2006). The current extent of tropical secondary forests is difficult to estimate, partly because of differences in definition of secondary forest. For the Global Forest Resources Assessment (FRA), the Food and Agriculture Organisation of the United Nations (FAO) uses the designation of "other naturally regenerating forest" for any non-planted forests with clear "visible signs of past or present human activity" (FAO, 2010). The FRA 2010 estimated that these forests account for 57% of the world's total forest area (FAO, 2010), and more than 80% of the tropical countries that provided data reported an area of "other naturally regenerating forests" exceeding that of primary forest (Chazdon, 2014). However, the definition used by the FAO is broad: it encompasses both degraded forests (after logging activity for instance) and forests re-establishing after another land use, two types of forests differing greatly in their structure, composition and dynamics (Putz & Redford, 2010; Chazdon, 2014). For the present study, I use "secondary forests" to refer exclusively to forests establishing after previous deforestation (Wright & Muller-Landau, 2006; Putz & Redford, 2010), which Chazdon (2014) prefers to call "second-growth" or "regenerating forests" to avoid ambiguity. To refer to forests with no signs of human activity, I prefer the more neutral term of "old-growth forests" to the terms "mature forests", "primary forests" or "pristine forests".

Because of the importance of their current and estimated future extent, it is important to understand the ecology of tropical secondary forests and their potential for biodiversity conservation and provision of ecosystem services. Secondary forests have an important role to play for the provision of regulating

and supporting ecosystem services[1]. They have a high capacity for carbon sequestration in biomass: Martin *et al.* (2013) estimated that tropical secondary forests can recover 83% the aboveground biomass stock of old-growth forest in 85 years (based on 326 secondary forest plots) and Poorter *et al.* (2016) estimated that neotropical secondary forests can recover 90% in an average of 66 years (based on 28 forest sites). Poorter *et al.* (2016) also found that the average aboveground carbon uptake rate over the first 20 years was 11 times that of old-growth forests (based on 44 sites). Belowground biomass stock seems to be slower to recover: Martin *et al.* (2013) found that it reaches only 50% of the stock of old-growth forests after 80 years (based on 76 plots). Trends for soil carbon are less clear: Martin found a very weak correlation between soil carbon and successional age, with soil carbon stocks in secondary forests similar to those in old-growth forests (185 plots), whereas Don *et al.* (2011) estimated that secondary forests store 9% less carbon in their soil than old-growth forests, using a definition of secondary forest that includes managed and partially exploited forests (71 studies). Although the provision of other ecological services has been less studied and not quantitatively synthesised, Chazdon (2014) reviewed evidence of their importance for many hydrological functions (such as evapotranspiration) and nitrogen fixation.

For biodiversity, several quantitative reviews show the capacity of secondary forests to recover levels of richness of animal and plant species similar to those of old-growth forests within a few decades. On the basis of 39 studies considering mainly insects and vertebrates, Dunn (2004) found that the animal species richness of tropical secondary forests can reach that of old-growth forests after two to four decades. Martin *et al.* (2013) estimated this recovery time to be five decades for tree species (based on 204 secondary forest plots) and to be more than a century for epiphyte species (based on 65 secondary forest plots). The rates of recovery of animal and plant species composition are however slower than species richness (Dunn, 2004; Martin *et al.*, 2013). Reviewing 65 studies, Dent and Wright (2009) showed that many animal species of old-growth forests can colonize secondary forests, but some highly specialised ones do not. These results, together with the predictions of Wright and Muller-Landau (2006) for future forest cover, support the potential of secondary forests to mitigate species extinction due to deforestation but suggest that secondary forests cannot fully replace old-growth in term of biodiversity conservation (Chazdon, 2014).

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1. as defined by the Millennium Ecosystem Assessment (2003)

1.2 Secondary succession in tropical forests

1.2.1 Models of forest succession: determinism and stochasticity

Succession has been a major focus of plant community ecology for more than a century (McIntosh, 1999), yet the processes underlying assembly of secondary forests continue to be actively researched (Norden *et al.*, 2015). The early view of Clements (1916) of deterministic and convergent succession towards a single state of equilibrium (monoclimax hypothesis), was highly holistic (Finegan, 1984) and drew an analogy between the development of an ecosystem and that of an organism. The relay floristics model (Egler, 1954), close to Clements' view, describes a successive replacement of species during succession, based on facilitation of the establishment of later successional species by earlier ones (facilitation model of Connell and Slatyer, 1977). Other more individualistic and reductionist models consider that all groups of species are present from the beginning of succession and successively assume dominance (the initial floristic composition model of Egler, 1954): either species of late succession become dominant by tolerating environmental conditions in which early successional species cannot survive (tolerance model of Connell and Slatyer, 1977), or species dominant earlier in succession inhibit the establishment of later ones (inhibition model of Connell and Slatyer, 1977) leading to "arrested succession". These deterministic models are all based on the idea that trade-offs between plant traits promote success in different stages of succession (Huston & Smith, 1987). The deterministic character of succession was challenged as early as the 1920s by Gleason (1926) who introduced the notion of unpredictability. Lawton (1987) proposed a model of succession based only on random survival of established species and colonisation by new species, paving the way for the neutral theory of community assembly (Hubbell, 2001). Although deterministic niche-based and neutral models have often been treated as mutually exclusive explanations for observed patterns of succession, a growing body of literature shows the importance of the integration of the two (Chave, 2004; Tilman, 2004; Gravel *et al.*, 2006; Norden *et al.*, 2015). The alternative stable states model combines elements of both: it states that an ecosystem can follow one of several possible successional trajectories, depending on past events and the timing of arrivals of organisms combined to some random events (Young *et al.*, 2001; Temperton & Hobbs, 2004). However, its general applicability to forest ecosystems has recently been challenged (Newton & Cantarello, 2015).

Moving away from the opposition between deterministic and neutral models of succession, the focus of research has shifted towards understanding the relative contribution of deterministic events and stochastic ones (Norden *et*

al., 2015) and assessing the factors affecting successional trajectories (Chazdon, 2003). The aim is now to understand if, and under what circumstances, secondary communities converge towards the state of the vegetation before disturbance or lead to alternative stable states (Young *et al.*, 2005; Norden *et al.*, 2009).

I therefore define forest succession as the set of changes (in structure, composition and functioning) occurring in an entire forest following a previous non-forested state, without making an *a priori* inference about its predictability. I focus on secondary succession, the form of succession that occurs on land where legacies of the previous ecosystem (such as soil or propagules) are still present, as opposed to primary succession (Chazdon, 2003). Forest re-establishing on land previously used for agricultural activities is the most common type of successional forests in the tropics (Chazdon *et al.*, 2007).

1.2.2 Factors influencing secondary succession in tropical forests

In this section, I present the multiple interacting factors that influence successional trajectories in tropical forests, at scales ranging from the region to the community. They first affect the early stages of succession, which in turn modify biotic and abiotic conditions for the later stages, and therefore have long-term effect on secondary forests (Figure 1). I provide examples from both wet and dry tropical forests (the distinct characteristics of tropical dry forests are highlighted in section 1.5).

Abiotic environmental factors

Several abiotic environmental factors can influence trajectories of secondary succession at scales ranging from the region to the site. The climate of the region affects successional trajectories: quantitative reviews have shown that precipitation regime affects the rate of aboveground biomass recovery (Becknell *et al.*, 2012; Poorter *et al.*, 2016) and the relative importance of vegetative *versus* seed reproduction (McDonald *et al.*, 2010). Soil properties of the site can affect the structure, dynamics, and species richness and composition of successional forests (Gehring *et al.*; Finegan & Delgado, 2000; Ceccon *et al.*, 2003; Ceccon *et al.*, 2004; Powers *et al.*, 2009).
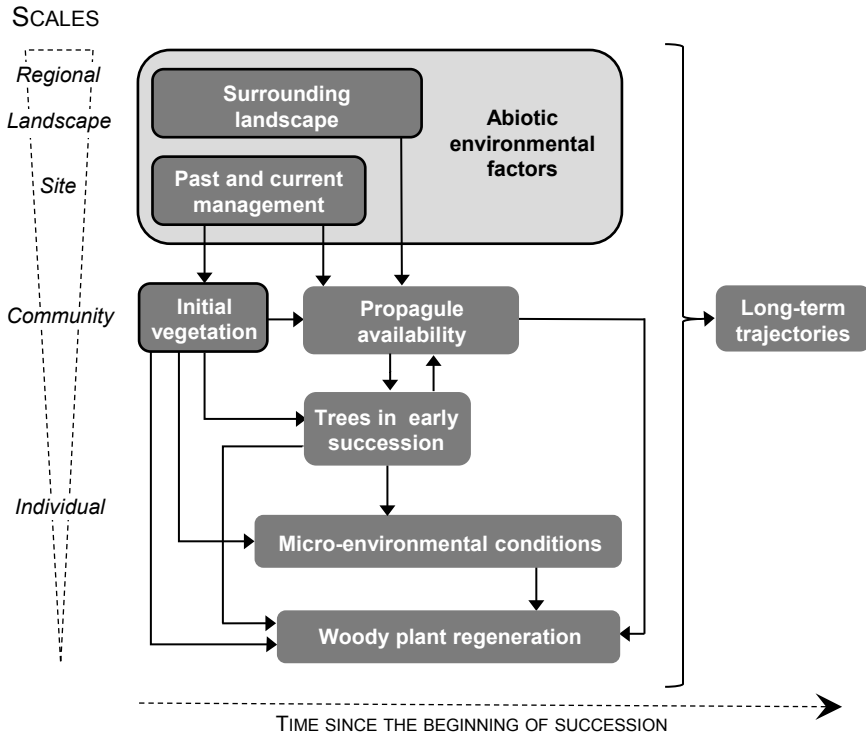
Figure 1. Conceptual framework of the factors influencing succession in tropical forests. Surrounding landscape and past and present management are not considered to be abiotic environmental factors but they act at spatial and temporal scales that partially overlap with these. Boxes encircled by a black line are the factors acting from the beginning of succession (discussed in this section).

Surrounding landscape

The composition of the surrounding landscape is important: nearby forests (old-growth forests and riparian vegetation) act as a source of seeds that can colonize the successional site (Chazdon, 2014). The distance to the nearest forest and area of forest in the landscape influences the structure and species diversity (Slocum & Horvitz, 2000; Griscom *et al.*, 2009; Sovu *et al.*, 2009; Duarte *et al.*, 2010; Gomes Reis Lopes *et al.*, 2012). The direction of the forest relative to the dominant winds can also affect the relative proportion of seeds with different dispersal syndromes dispersed into successional forests (Janzen, 2002; Castillo-Nunez *et al.*, 2011). Scattered trees and live-fences improve seed dispersal in the landscape by acting as stepping stones and corridors for animal dispersers (Estrada *et al.*, 1993; Chazdon *et al.*, 2011).

Past and current management

Past and current management affects successional trajectories. The type of land use before its abandonment has an effect on the structure and rate of biomass accumulation, the species richness and composition, and the relative proportion of dispersal syndromes of the plants in successional forests (Ferguson *et al.*, 2003; Larkin *et al.*, 2012; Martin *et al.*, 2013). This is due to several reasons: different past land uses have different impact on the soil (*e.g.* compaction, erosion, fertility) (Maass *et al.*, 1988; De Wilde *et al.*, 2012). The vegetation present at the time of abandonment also differs between past land uses (this point is developed in the next paragraph). The duration and intensity of the previous land use are also important factors (Pereira *et al.*, 2003; Sovu *et al.*, 2009). Fire, used for management purposes or accidental, occurring before or after the abandonment of the previous land use decreases species richness and changes the species composition by favouring fire-tolerant species and species capable of resprouting (Rico-Gray & Garcia-Franco, 1992; Marod *et al.*, 2002; Hooper *et al.*, 2004). When fire is especially intense it can severely reduce regeneration by destroying the soil seed bank and killing roots (Kennard *et al.*, 2002). Grazing occurring in successional forests decreases biomass and species accumulation (Griscom *et al.*, 2009), alters species composition (Stern *et al.*, 2002) and can also have the beneficial effect of grass control (Blackmore & Vitousek, 2000; Janzen, 2002; Stern *et al.*, 2002; Larkin *et al.*, 2012). Lastly, restoration activities also affect successional trajectories (see section 1.6).

Initial vegetation

The vegetation *in situ* at the beginning of succession influences the establishment of woody vegetation. Grasses, and especially highly productive exotic species planted in pasture sites, have an overall negative effect on the regeneration of woody plants. Because of their high seed dormancy capacity, some herbaceous species can remain dominant in the soil seed bank a long time after the beginning of succession (Martins & Engel, 2007; Maza-Villalobos *et al.*, 2011b). In many cases, grass reduces or removes the capacity of woody species to establish by competing with them for resources (Cabin *et al.*, 2000; Cabin *et al.*, 2002b; Ferguson *et al.*, 2003; Hooper, 2008; Griscom *et al.*, 2009; Thaxton *et al.*, 2012; Wolfe & Van Bloem, 2012). Moreover, grass is a highly combustible fuel biomass and can increase the risk of fire incidence and its intensity (D'Antonio & Vitousek, 1992; Blackmore & Vitousek, 2000). However, in some cases, grasses can provide suitable conditions for woody species establishment (Hardwick *et al.*, 1997; Esquivel *et al.*, 2008). Woody vegetation present at the beginning of succession, such as isolated trees in pastures and remnant trees in land under shifting cultivation, can enhance

regeneration of woody species (Guevara *et al.*, 1992; Carrière *et al.*, 2002b; Schlawin & Zahawi, 2008) through resprouting (Kammesheidt, 1999; Sampaio, 2007), input of seeds (directly or through attraction of animal dispersers) (Guevara *et al.*, 1986; Slocum & Horvitz, 2000; Carrière *et al.*, 2002a; Chazdon, 2014) and amelioration of microclimate (Duarte *et al.*, 2010). Remnant trees can have long-lasting effects (at least 20 years after beginning of succession) on the species diversity and composition of secondary forests through their impact on the regeneration process (Sandor & Chazdon, 2014).

1.3 Importance of plant-plant interactions for succession

In this section, I present the different types of plant-plant interactions and explain their importance for succession. I do not review empirical evidence of plant-plant interactions during succession as this is done for tropical dry forests in paper I and summarised in section 4.1.

1.3.1 Types of plant-plant interactions

Plant-plant interactions are processes by which a plant influences the establishment and fitness of other plants, positively (facilitation) or negatively (competition). They can have an effect on ecological processes and patterns from the individual to the landscape scale (Bruno *et al.*, 2003), and are therefore important in structuring plant populations and communities (Bertness & Callaway, 1994).

Competitive interactions have been much more studied yet facilitative interactions have received increasing interest since the 1990s (Michalet & Pugnaire, 2016). Facilitation and competition often co-occur in the same community and the balance between these processes is complex (Callaway & Walker, 1997). It can depend on the intensity of abiotic constraints: Grime (1979) suggested that competition was more important in high productivity environments. Conversely Bertness and Callaway (1994) made the hypothesis that facilitation was more important in environments with high abiotic stress or high consumer pressure. This hypothesis, called the stress gradient hypothesis, has been supported by a number of meta-analyses (*e.g.* Lortie and Callaway 2006; He *et al.* 2013) but challenged by other studies (Maestre *et al.*, 2005; Soliveres & Maestre, 2014; Butterfield *et al.*, 2016), and empirical evidence suggests that beyond a threshold of harshness of environmental conditions competition can overtake facilitation and result in a negative net effect on plant performance (Maestre & Cortina, 2004; Siles *et al.*, 2010). The outcome of plant-plant interactions can also depend on the life stages (Callaway & Walker, 1997): suitable conditions for the younger stages of a plant's regeneration cycle

can be unsuitable for its adult stage (Grubb, 1977) and the outcome of plant-plant interactions can change from facilitative to competitive during the life of a plant. Finally, Ganade *et al.* (2008) suggest that there can be an interplay of the stress gradient hypothesis and the effect of life stage.

Another way of looking at plant-plant interactions is to consider the mechanisms underlying them. Direct interactions happen through modification of the abiotic environment (light, temperature, soil moisture, chemical or physical properties) whereas indirect interactions happen through a third organism (*e.g.* herbivore, pollinator, seed disperser, mycorrhizal fungus or soil microbe) (Callaway, 1995; Bruno *et al.*, 2003; Callaway, 2007).

1.3.2 Core processes for deterministic niche-based models of succession

Plant-plant interactions are central to deterministic niche-based models of succession. The model of Clements (1916) and the facilitation model of Connell and Slatyer (1977) are based on an amelioration of environmental conditions by early successional species (*i.e.* species that establish and dominate at early stages of succession) for late successional species, whereas the tolerance and inhibition models (Connell & Slatyer, 1977) are based on negative interactions. The realised niche is often viewed as the set of environmental conditions in which a species can establish, considering biotic interactions with other species (Bruno *et al.*, 2003). Facilitation can therefore result in an expansion of the realised niche and competition in a reduction (Bruno *et al.*, 2003; Callaway, 2007; Bulleri *et al.*, 2016).

The nurse plant effect, defined as facilitation of the recruitment of plants under the canopy of other plants (Callaway & Walker, 1997; Rodríguez-Echeverría *et al.*, 2016), is commonly observed during succession in tropical forests. Shrubs, such as the nitrogen fixing *Leucaena leucocephala* in Puerto Rico (Molina Colon & Lugo, 2006; Santiago-Garcia *et al.*, 2008; Wolfe & Van Bloem, 2012) and *Chromolaena odorata* in West Africa (Kassi N'Dja & Decocq, 2008), or trees, such as several species of *Mimosa* or *Guazuma ulmifolia* in Mesoamerica (Romero-Duque *et al.*, 2007; Lebrija-Trejos *et al.*, 2008; Williams-Linera *et al.*, 2011), can facilitate the establishment of other species under their cover. On the other hand, the inhibition of woody species by grass after abandonments of pasture sites (described in section 1.2.2) is an example of negative interactions.

1.4 Species-based and functional trait-based approaches

1.4.1 From context-specific accuracy to global comparisons

The taxonomic approach, giving a central role to the species, has long been the main approach adopted in community ecology (McGill *et al.*, 2006). This approach focusses on species-specific requirement and pairwise interactions between species (McGill *et al.*, 2006). It is particularly valuable for conservation, restoration and management. It allows emphasis to be placed on species that are seen as having high conservation value, such as highly threatened (IUCN, 2015) or emblematic species (Clark & May, 2002; Sergio *et al.*, 2006), identification of geographical priorities for conservation (Myers *et al.*, 2000; Jenkins *et al.*, 2013) and guiding of management practices (such as species choice by practitioners). However, the species-based approach has several limitations. (1) It relies on the assumption that the species level is the most appropriate level to understand plant ecology, in other words that most of the variation of traits related to plant fitness and function is greater between species. This is challenged by the hypothesis of phylogenetic conservatism suggesting that higher taxonomic levels can be more relevant (Ackerly, 1999), and by an increasing number of studies showing substantial variation in trait values within species (this point is detailed in section 1.4.3). (2) The species-based approach reaches its limits of practicality in species rich ecosystems, such as tropical forests. (3) The highly context-specific and locally-contingent understanding of ecological processes resulting from this approach impedes comparison between sites and assessment of general patterns of community assembly and functioning (Duarte *et al.*, 1995; Simberloff, 2004; McGill *et al.*, 2006).

Non-taxonomic approaches are based on the idea that species are not functionally unique entities (Duarte *et al.*, 1995). Using the characteristics of plants, rather than their taxonomic identity, to classify them and understand their function is not a new approach (Garnier *et al.*, 2016). This approach has developed over the last century, notably with the work of Raunkiaer (1934), Grime (1979) and Noble and Slatyer (1980) and has gained momentum in the last two decades with the increasing number of studies based on functional traits[2]. Functional traits are defined as "any morphological, physiological or phenological feature measurable at the individual level" (Violle *et al.*, 2007) and relate to the function and fitness of organisms (Lavorel & Garnier, 2002; McGill *et al.*, 2006; Violle *et al.*, 2007). They can provide mechanistic answers

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[2]. See the post of Brian McGill on the blog *Dynamic ecology*
(https://dynamicecology.wordpress.com/2015/07/01/steering-the-trait-bandwagon/)

to questions ranging from the individual and population scales, such as those relating to predicting the performance and fitness of plants (Reich *et al.*, 2003; Wright *et al.*, 2010), to the ecosystem scale, such as assessing ecosystem functioning (Tilman *et al.*, 1997; Diaz & Cabido, 2001; Lavorel & Garnier, 2002) and services (Diaz *et al.*, 2007). At the community scale, the functional trait-based approach provides information about community assembly. Mean trait values can be used to understand how environmental gradients structure plant communities (Lohbeck *et al.*, 2013; Fortunel *et al.*, 2014). Characteristics of the distribution of traits in a community can help in assessing the importance of abiotic environmental filtering (expected to produce under-dispersed trait distribution), and competition, leading to niche differentiation between species (hypothesis of "limiting similarity", expected to produce over-dispersed trait distribution) (Chesson, 2000; Cornwell *et al.*, 2006). However, competition can also result in under-dispersed trait distribution (as does abiotic environmental filtering) through "equalizing mechanisms" (Chesson, 2000). Consideration of different types of traits (resource acquisition traits *versus* regeneration traits) and the types of null model used to test hypotheses can help distinguish between these different mechanisms (Grime, 2006; Bernard-Verdier *et al.*, 2012).

By providing an approach based on a limited number of traits, as an alternative to a high number of species, the functional trait approach reduces the dimensionality and complexity of plant communities (McNamara *et al.*, 2012; Laughlin, 2014). Furthermore, most traits can be measured in any plants worldwide while the set of species present in a community is dependent on the local species pool. As a result, the great value of the trait-based approach is the potential for global comparisons to determine which trends of plant community responses to, and effects on, their environment are common among plant communities globally, and which are more locally specific (Duarte *et al.*, 1995; Reich *et al.*, 1997; McGill *et al.*, 2006).

1.4.2 Functional traits and plant strategies

The identification of plant strategies which summarise the capacity of plant species to establish and reproduce in a given environment (Grime, 1979), is an approach to using functional traits that further reduces dimensionality (Laughlin, 2014). Discrete classifications of species according to their resource requirements, such as guilds (Root, 1967) and functional groups (Cummins, 1974), have progressively lost their importance with the increasing emphasis on continuous spectra of strategies (Laughlin, 2014). In the framework of Grime (1979), species' strategies are located inside a triangle with its three corners being competitive, stress-tolerance and ruderal strategies respectively

(the "C-S-R triangle theory"). The exact position of a species in the triangle is defined by its traits and corresponds to its relative tendency to fit each of these strategies; "generalist" species are located in the centre.

The exploration of correlations among functional traits allows the identification of the main axes defining the patterns of trait variations and, potentially, the trade-off between strategies (Laughlin, 2014). Westoby (1998) proposed a three dimensional scheme based on just three functional traits: specific leaf area (SLA), height of the plant at maturity and seed mass (the "LHS" scheme). These traits represent three main axes of trait variation termed: resource economics, stature and regeneration (Garnier *et al.*, 2016). In a recent study on the largest sample of plant species ever analysed, Díaz *et al.* (2016) considered six important traits related to growth, survival and regeneration and showed that most of their variation was accounted for by just two axes: the first being defined by plant and propagule sizes (with short species tending to have small propagules) and the second related to leaf resource economics (explained below). Although the intrinsic number of axes of variation in functional traits remains an open question, Laughlin (2014) found it to be higher than the three proposed by Westoby (1998). Laughlin (2014) used a variety of methods to estimate dimensionality of three different datasets and found that their median dimensionality ranged between four and six. He recommends the use of traits of several organs and the consideration of additional types of traits, such a phenological and life-history traits.

The axis of trait variation that has been developed and tested with most empirical evidence is that of leaf resource economics. This is the axis that I focus on in paper IV. Wright *et al.* (2004) showed the evidence for a main axis of leaf functional traits across plants worldwide, which has been called the leaf economics spectrum. At one end of this spectrum are productive strategies with a fast return on investment of resources in leaves characterized by high leaf nutrient concentrations, high metabolic rates and short leaf lifespan, also called acquisitive strategies (Reich, 2014). At the other end, conservative strategies, with a slow return on investment, are characterized by low metabolic rates, and expensive leaf construction and defence costs allowing a longer leaf lifespan. There is also evidence for one main axis representing variation in such economics strategies for other plant organs: stems (Reich *et al.*, 2003; Chave *et al.*, 2009) and roots (Prieto *et al.*, 2015; Roumet *et al.*, 2016). Reich (2014) propose the integration of the economics spectra of organs into a whole-plant economics spectrum defined by the variation between slow/conservative and fast/acquisitive strategies, although empirical results show decoupling of these spectra (Baraloto *et al.*, 2010b). In line with the hypothesis of Grime (1979) that there is a positive correlation of the capacities of a species to acquire

different resources, Reich (2014) provides evidences for the association of these spectra with all resources gradients (light, water, nutrients); acquisitive strategies being advantageous in high resource environments and conservative strategies enhancing survival in low resource environments.

1.4.3 Variation of functional trait values within and among species

Although functional traits are defined as features measured at the scale of individuals (Violle *et al.*, 2007), most functional trait-based studies in community ecology overlook the variation in trait values occurring within species (Violle *et al.*, 2012), following the idea that "to be useful to community ecology, traits should vary more between than within species" (McGill *et al.*, 2006). Standard protocols recommend sampling a limited number of individuals per species in standardised environmental conditions (Cornelissen *et al.*, 2003; Perez-Harguindeguy *et al.*, 2013) and calculating a mean value per species from these which is used to calculate functional diversity indices of communities (Laliberte & Legendre, 2010; Mouchet *et al.*, 2010). However, this approach is increasingly challenged and there is growing recognition of the importance of intraspecific variation of functional trait values (Lepš *et al.*, 2011; Violle *et al.*, 2012; Laughlin & Messier, 2015).

Several studies have shown that variation of trait values within species is not negligible compared with variation between species. Siefert *et al.* (2015) carried out a meta-analysis of 629 plant communities worldwide for 36 functional traits and showed that intraspecific variation accounted for an average of 25% of the total trait variation within communities and 32% of the total trait variation across communities. For tropical forests, Messier *et al.* (2010) and Hulshof and Swenson (2010) partitioned the variance of trait values for commonly measured leaf functional traits across nested scales[3]. Messier *et al.* (2010) found that intraspecific variance accounted for 48% of the total variance of trait values for SLA and leaf dry matter content (LDMC), and Hulshof and Swenson (2010) found that the contribution of intraspecific variance ranged from 35 to 68% of the total variation (for leaf area, dry mass, SLA and leaf water content).

Intraspecific variation of functional trait values can result from both the genetic variation between individuals and the capacity of a genotype to express different phenotypes (Violle *et al.*, 2012; Garnier *et al.*, 2016). The latter can occur as a response to variation in environmental conditions in space or in time (*e.g.* between seasons, Gotsch *et al.*, 2010) (Violle *et al.*, 2012), which is called

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[3]. *N.B.* The results of such studies partitioning the variance of trait values across scales are highly dependent on methodological choices (sampling design and number and order of nested levels considered) (Messier *et al.*, 2010) and therefore need to be compared with caution.

phenotypic plasticity (Valladares *et al.*, 2006). Genetic variability and phenotypic plasticity are difficult to disentangle without experimental studies, but doing so is not essential for community studies because both mechanisms can be a response to environmental conditions (Violle *et al.*, 2012), although over different time scales (natural selection by past conditions over a long evolutionary time scale for genetic variability and changes at the scale of the life of an individual for phenotypic plasticity). The phenotypes expressed by a given genotype can also change with the development of a plant (ontogeny) (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014).

The importance of considering intraspecific variation for studies of community ecology is supported by both theoretical arguments and empirical evidence. Treating species' functional trait values as discrete single values (*e.g.* by using species mean value) gives average information on the environmental requirements of species (Violle *et al.*, 2012). Considering it as the within-species distribution (*i.e.* the distribution of trait values measured on different individuals of the same species) provides information on a species' capacity to establish and thrive in different conditions of resource availability and interactions with neighbouring plants (Violle *et al.*, 2012; Laughlin & Messier, 2015). This latter approach provides a better assessment of the niche of a species, which is important in community ecology to understand mechanisms of species coexistence and community assembly. Including intraspecific variation of functional trait values can therefore provide a better understanding of abiotic and biotic drivers of community assembly (Violle *et al.*, 2012). This is supported by empirical evidence: several studies have shown that intraspecific variation can be important in explaining community variation along environmental gradients (*e.g.* Lepš *et al.*, 2011; Carlucci *et al.*, 2015). Furthermore, observed patterns in interspecific variation, such as trait correlations (Laughlin & Messier, 2015) or direction of change along environmental gradients (Albert *et al.*, 2010; Lepš *et al.*, 2011; Kichenin *et al.*, 2013), do not necessarily hold for intraspecific variation. These are reasons in favour of a change from a species-based to an individual-based approach to community ecology. Ultimately this could lead to species identity having a much diminished importance (Messier *et al.*, 2010). However, there are good theoretical and empirical reasons for considering both interspecific and intraspecific variation, which is the approach I use for paper IV. (1) Phylogenetic conservatism of trait values predicts that individuals that are phylogenetically close should have close trait values, therefore it supports the importance of the species and higher phylogenetic levels (Ackerly, 1999). (2) Many studies show that the interspecific level is the one where the highest variation is found (*e.g.* Markesteijn *et al.*, 2007; Hulshof and Swenson, 2010;

Powers and Tiffin, 2010). (3) A sampling approach based solely on individuals would require the measurement of traits on all individuals in a community (Violle *et al.*, 2012), which is difficult in practice. It is important to move from the use of a single trait value per species across all communities to a separate value per species per community (Baraloto *et al.*, 2010a; Lepš *et al.*, 2011). At present there is an urgent need for studies that identify the circumstances under which it is important to consider intraspecific variation, such as that of Spasojevic *et al.* (2016).

1.5 Tropical dry forests

1.5.1 Definitions, distribution and state of conservation

There are several definitions of tropical dry forests. Mooney *et al.* (1995) merely define tropical dry forests as "forests occurring in tropical regions where there are several months of severe, even absolute, drought". Most definitions are based on a range of mean annual precipitation, *e.g.* 250-2000 mm (Murphy & Lugo, 1986), 400-1700 mm (Gerhardt & Hytteborn, 1992), 500-2000 mm (Holdridge, 1967; Becknell *et al.*, 2012) or 700-2000 mm (Sanchez-Azofeifa *et al.*, 2005), and some definitions also use a minimum mean annual temperature, 17 °C (Holdridge, 1967) or 25 °C (Sanchez-Azofeifa *et al.*, 2005). As well as these two, Holdridge (1967) based his definition on a third variable, the annual ratio of potential evapotranspiration to precipitation (> 1). Other definitions consider a minimum number of dry months[4], *e.g.* three (Sanchez-Azofeifa *et al.*, 2005), four (Becknell *et al.*, 2012) or ~ six (Gerhardt & Hytteborn, 1992). For the present study, I define tropical dry forests as forests with a mean annual precipitation of 500-2000 mm, a mean annual temperature > 17 °C and at least three dry months (monthly precipitation < 100 mm).

Although the seasonality of precipitation is a major environmental factor affecting the ecological processes of both tropical dry forests and savannas, they are distinct vegetation types differing in their structure and ecology (Dexter *et al.*, 2015; Veenendaal *et al.*, 2015). In the Neotropics, they also have distinct floristic compositions (Pérez-García & Meave, 2006; Dexter *et al.*, 2015). While tropical dry forests are dominated by trees, and have a relatively closed canopy and a higher aboveground biomass, savannas are more open and are characterised by the presence of an abundant grass layer (Pennington *et al.*,

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[4] There is generally no precipitation during the dry months. Many definitions of tropical dry forests do not specify a definition of dry month. Sanchez-Azofeifa *et al.* (2005) define it as a month with < 100 mm precipitation.

2000; Pennington *et al.*, 2006; Pennington *et al.*, 2009; Veenendaal *et al.*, 2015), usually of species with a C4 photosynthetic pathway (Dexter *et al.*, 2015). Tropical dry forests and savannas can occur under similar climatic conditions and therefore often co-exist in the same area (Pennington *et al.*, 2006; Pennington *et al.*, 2009). Their structural and floristic differences are, however, the results of distinct environmental drivers that have shaped the evolution of their distinct floristic assemblages (Furley, 2007). Fire is considered to be the major environmental factor responsible for the differences in the ecology of these two vegetation types: while natural fire is an essential part of the ecology of savannas, tropical dry forests usually do not experience fire, except when caused by human activities (Hughes *et al.*, 2013; Dexter *et al.*, 2015). As a consequence of their different environmental drivers, forest and savanna plant species have different sets of trait values. Savanna species are generally more tolerant of fire due to adaptions such as thick and corky bark, protected buds, and large investment in carbohydrate reserves and high root biomass allowing them to quickly resprout after a fire. In contrast, forest species usually lack these adaptations but have a faster growth rate enhancing their competitiveness in the denser forest environment, as well as the ability to regenerate under a closed canopy (Hoffmann, 2000; Pennington *et al.*, 2000; Furley, 2007; Pennington *et al.*, 2009; Hoffmann *et al.*, 2012).

A number of studies have shown that savannas can transition to forests in the absence of fire, or conversely that forests can become savannas under the influence of anthropogenic fires (Hoffmann *et al.*, 2012; Veenendaal *et al.*, 2015). Savannas and tropical dry forests can therefore be seen as alternative stable states governed by fire (Veenendaal *et al.*, 2015). Hoffmann *et al.* (2012) propose two types of threshold for the transition between savannas and forests: the fire-resistance threshold characterised by the accumulation of bark that avoids stem death, and the fire-suppression threshold reached when the canopy cover is sufficient to exclude the fire-prone grass layer. Since savanna tree species accumulate bark more quickly than forest species, and forest species form a closed canopy more quickly than savanna species, Hoffmann *et al.* (2012) state that species traits are important in influencing the transition between the two vegetation types. Moreover, the amount of resource available also affects this transition: resource-rich sites can allow both the fire-resistance and the fire-suppression thresholds to be reached more quickly (Hoffmann *et al.*, 2012), explaining why forests generally occur on more fertile soil than savannas (Pennington *et al.*, 2000; Linares-Palomino *et al.*, 2003; Pennington *et al.*, 2006). Fire and soil fertility are therefore the two main interacting abiotic factors affecting the occurrence of forest or savanna in seasonality dry tropical climates (Veenendaal *et al.*, 2015).

Tropical dry forests[5] represent 42% of the extent of the world's tropical forests (Murphy & Lugo, 1986). Miles *et al.* (2006) estimate that they cover a total of more than 1 million km^2 across the three tropical regions, the majority of which is in the Neotropics (66.7%)[6]. Because of their attractive climate for human activities, they have been extensively deforested (Murphy & Lugo, 1986; Maass, 1995) and their current extent covers only a fraction of their original one (Aronson *et al.*, 2005). At the end of the 1980s, Janzen (1988) declared that tropical dry forest was "the most endangered major tropical ecosystem". Unfortunately, tropical dry forest continues to be endangered; Miles *et al.* (2006) estimated that 97% of the current area of tropical dry forest is subject to one or more of the following threats: climate change, forest fragmentation, fire, conversion to agriculture and human population growth. Despite these threats, much less research has been conducted in tropical dry forests compared with moister ones (Sanchez-Azofeifa *et al.*, 2005; Vieira & Scariot, 2006b; Quesada *et al.*, 2009). A good understanding of how their environmental characteristics affect their dynamics is therefore important for their conservation and restoration.

1.5.2 Highly seasonal environment

> "The dry forest may appear uniformly green during the rainy season, but during the dry season this homogeneity changes into a complex mosaic of tens of habitat types distinguished by the different drying rates of different soils and exposures, different ages of succession, and different vegetation types." (Janzen, 1988, p. 131)

The strong seasonality of precipitation is the most characteristic feature of tropical dry forests (Mooney *et al.*, 1995). The alternation of a dry season with virtually no rain, high irradiance and high evaporative demand and a wet season with high precipitation controls the timing of vegetative and reproductive processes (Murphy & Lugo, 1986; Janzen, 1988; Holbrook *et al.*, 1995; Quesada *et al.*, 2009; Maass & Burgos, 2011), leading to striking differences in the forest environment between seasons (Figure 2). In tropical dry forests, the factors limiting plant performance therefore change between seasons from water-limitation during the dry season to light-limitation during the wet season.

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[5] *sensu* Holdridge (1967)

[6] *N.B.* Miles *et al.* (2006) restrict their definition of forest to areas with at least 40% tree cover, which is likely to exclude most savanna and miombo areas.
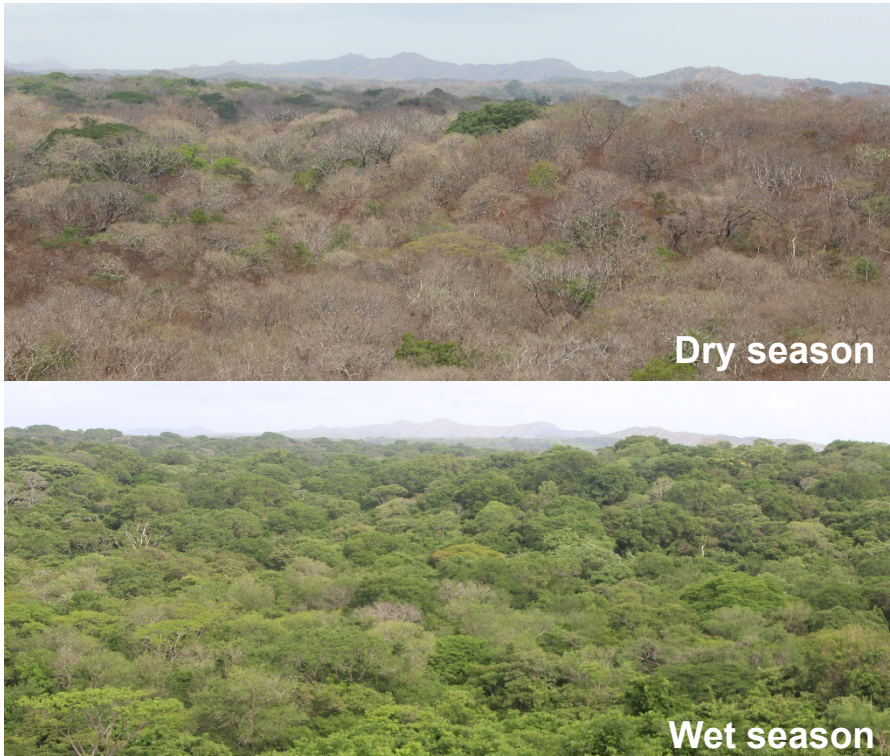
Figure 2. Contrasting green leaf cover between seasons in tropical dry forest. Photos taken from *mirador Tierras Emergidas* (Santa Rosa, Costa Rica) on 10/05/14 (dry season) and 01/07/14 (wet season) (photos Géraldine Derroire).

Most growth of tropical dry forests trees occurs during the wet season (Lopezaraiza-Mikel *et al.*, 2013). The consequence of this limited duration of the growing period is a generally lower net primary productivity than in moister forests (Murphy & Lugo, 1986; Vieira & Scariot, 2006b). Several plant strategies linked to greater tolerance of water limitation during the dry season coexist in tropical dry forests (Giraldo & Holbrook, 2011): woody plants have leaf phenological patterns ranging along a gradient of deciduousness (Frankie *et al.*, 1974; Opler *et al.*, 1980b; Borchert, 1994). The patterns of correlation between leaf phenological habit (*i.e.* evergreen or deciduous character) and other plant functional traits is still insufficiently understood (Hulshof *et al.*, 2013). Some studies show that deciduous trees have leaf trait values associated with the acquisitive end of the leaf economics spectrum (Sobrado, 1991; Pringle *et al.*, 2011), while other studies show a great overlap of functional trait values between deciduous and evergreen trees (Brodribb & Holbrook, 2004; Powers & Tiffin, 2010). The relationship between rooting depth of trees and their leaf phenology is also variable (Giraldo & Holbrook, 2011). The seasonal

changes in canopy openness resulting from tree deciduousness lead to contrasted microclimatic conditions in the understorey (Parker *et al.*, 2005; Lebrija-Trejos *et al.*, 2011).

The seasonality of precipitation also influences reproductive phenology. There is a peak of flowering in each season (Justiniano & Fredericksen, 2000; Frankie *et al.*, 2004) and the timing of flowering depends on resource allocation between vegetative and reproductive processes (Borchert, 1983; Singh & Kushwaha, 2006) and on the pollination agent (Frankie *et al.*, 2004). The timing of fruiting is mainly linked to the dispersal syndrome: seeds dispersed by wind (anemochory) or gravity tend to be produced during the dry season while fleshy-fruited zoochorous species fruit mainly during the rainy season (Ray & Brown, 1994; Sobral Griz & Machado, 2001; Vieira & Scariot, 2006b; Vieira *et al.*, 2008). Most seeds remain dormant until the beginning of the wet season when there is a peak of germination, as found by Garwood (1983) in the seasonal tropical moist forest of Barro Colorado Island. Seedlings emerging early in the wet season can experience a longer growth period before the next dry season, which reduces their mortality (Van Schaik *et al.*, 1993; Khurana & Singh, 2001; Vieira & Scariot, 2006b).

1.5.3 Specificities of regeneration in tropical dry forests

The soil seed bank of tropical dry forests has a low density of accumulated seeds of woody species (Skoglund, 1992; Janzen, 2002). Seeds tend to germinate in the year following their production (Janzen, 2002). Seeds are also lost due to predation, desiccation or fire (Skoglund, 1992; Janzen, 2002; Kennard *et al.*, 2002; Maza-Villalobos *et al.*, 2011b). The soil seed bank therefore has a limited role in the re-establishment of forests through natural processes after another use of the land (Janzen, 2002; Kennard *et al.*, 2002; Lemenih & Teketay, 2005; González-Rivas *et al.*, 2009; Maza-Villalobos *et al.*, 2011b), and secondary succession is generally dependent on other sources of propagules.

Anemochory is a more important mode of seed dispersal in tropical dry forests than in moister ones (Gentry, 1995; Janzen, 2002). Vieira and Scariot (2006b) reported percentages of anemochorous species in several neotropical dry forests ranging from 30% to ~ 60% whereas this percentage was less than 20% in wet and moist forests. Anemochorous species are particularly important for secondary succession because their seeds can travel longer distances in fragmented landscapes and open areas than seeds of zoochorous species (Cubiña & Aide, 2001; Janzen, 2002; Castillo-Nunez *et al.*, 2011). They also tend to be less prone to desiccation than seeds of fleshy fruits (Vieira & Scariot, 2006b), which increases their survival in open areas.

Vegetative reproduction through resprouting is an important mode of regeneration in tropical dry forests (Ewel, 1977; Vieira & Scariot, 2006b). Resprouts can benefit from a more developed root system than seedlings, which allows better acquisition of soil resources, and, in some cases, from reallocation of carbohydrates stored in the roots, which can increase growth and survival rates in the early stage of establishment (Kennard *et al.*, 2002). This mode of regeneration is therefore the one most commonly observed after disturbance events that leave stumps or belowground stem or root tissue, although the importance of vegetative regeneration depends on the precipitation regime and the intensity of disturbance (Sampaio *et al.*, 1993; Kennard *et al.*, 2002; McDonald *et al.*, 2010).

Several authors have suggested that the gap dynamics model, which emphasises the importance of canopy gaps for regeneration in tropical wet forest, may not apply to tropical dry forests (Quesada *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a; Lévesque *et al.*, 2011). Several reasons are proposed for this difference. (1) Because of their more open canopy, light availability may be less limiting for seedling establishment in tropical dry forest, and the shade provided by the canopy may actually improve seed germination and seedling survival rate (Hardwick *et al.*, 1997; Teketay, 1997; Hoffmann, 2000; Cabin *et al.*, 2002a; McLaren & McDonald, 2003a; McLaren & McDonald, 2003b; Vieira *et al.*, 2006; Santiago-Garcia *et al.*, 2008; Wolfe & Van Bloem, 2012). (2) Resprouting is often considered to be a more common regeneration mode in tropical dry forests, as shown by Ewel (1977) who compared wet and dry forest sites in Costa Rica and Puerto Rico, and supported by many study reporting high rates of resprouting in tropical dry forests (as reviewed by Vieira and Scariot, 2006b). Reviewing a number of studies in tropical dry forests, McDonald *et al.* (2010) also showed that resprouting was more common in the drier sites. (3) Tropical dry forests are expected to have a lower rate of canopy gap formation then moister forests. Dickinson *et al.* (2001) found a low occurrence of tree uprooting in tropical dry forests, which they attributed to higher stability of trees due to their shorter stature, higher root-to-shot ratio, lower epiphyte load and lower frequency of storms. However, other evidence from tropical dry forests may actually support the effect of canopy gaps on regeneration. Dechnik-Vazquez *et al.* (2016) found a higher number of individuals and species of seedlings in gaps than under closed canopy, but no difference in species composition. Diamond and Ross (2016) found that the seedlings in canopy gaps generally belonged to late-successional species.

1.5.4 Changes during succession in tropical dry forests

The structure of tropical dry forests changes quickly in the early stages of secondary succession. Based on a quantitative review of 44 studies, Becknell *et al.* (2012) showed a rapid increase in aboveground biomass in the first two decades of succession followed by a slower increase. Similar trends have been found for crown area and basal area (Sovu *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a; Dupuy *et al.*, 2012). The rate of increase of components of forest structure depends on soil characteristics (Powers *et al.*, 2009), distance to old-growth forests (Gomes Reis Lopes *et al.*, 2012) and the intensity of disturbance caused by the previous land use (Molina Colon & Lugo, 2006; Romero-Duque *et al.*, 2007). Becknell *et al.* (2012) showed that aboveground biomass recovered within three to five decades. The amount of biomass depended on the mean annual precipitation of the area, with higher biomass in moister areas, but the time needed to reach it did not. I do not review here the changes in species richness and composition because this is the subject of the meta-analysis presented in paper II and summarized in section 4.2.

These structural changes have obvious consequences for the forest microclimate, yet they are rarely quantified. The only study of which I am aware is that of Lebrija-Trejos *et al.* (2011), who studied a 60-year chronosequence in Mexico. They found that understorey light levels and air and soil temperatures decreased while relative humidity increased, during succession. Soil water availability showed an initial increase followed by a decrease, probably as a result of increased transpiration of canopy trees. More studies on the changes in environmental conditions during succession are needed.

In comparison with moister tropical forests, aboveground biomass generally accumulates at a lower absolute rate in tropical dry forests (Ewel, 1977; Poorter *et al.*, 2016). However, because the quantity of biomass and basal area in old-growth forests is also lower in drier forests (Murphy & Lugo, 1986; Poorter *et al.*, 2016), the time needed to recover the structure of an old-growth forest in tropical dry forest can be similar to that in moister forests (Quesada *et al.*, 2009; Poorter *et al.*, 2016).

Because of their generally lower structural complexity, the difference in understorey light levels between the early and later stages of succession is smaller in tropical dry forests than in moister forests, and the changes in temperature and humidity may be stronger drivers of change in plant communities during succession (Lebrija-Trejos *et al.*, 2010b; Lebrija-Trejos *et al.*, 2011). As a result, the change in plant strategies during succession is expected to differ between tropical dry and moister forests (Lohbeck *et al.*, 2013; Letcher *et al.*, 2015). In tropical wet forests, the decrease in understorey

light availability with succession leads to a change from acquisitive to conservative strategies (Boukili, 2013; Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015). However in tropical dry forests, the high drought tolerance generally associated with conservative strategies (Reich, 2014) can reduce mortality in the face of high evaporative demand in early successional environments, which suggests a change from conservative to acquisitive strategies with succession. This hypothesis has only received mixed support from field studies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013; Becknell & Powers, 2014; Buzzard *et al.*, 2015), and leaf phenological habit and morphological traits that contribute to leaf cooling and control of water status can be more important in explaining changes in community functional composition during succession than those traits generally associated with leaf economics strategies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2015).

1.6 Ecological restoration in tropical forests

Ecological restoration, "assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2016), can increase biodiversity and the delivery of ecosystem services (Chazdon, 2008; Holl, 2012). Ecological restoration requires a good understanding of ecological processes (Hardwick *et al.*, 2004; Aronson & Vallejo, 2008; Holl & Aide, 2011), among which succession is of the utmost importance (Palmer *et al.*, 1997; Young, 2000; Hobbs *et al.*, 2007). Indeed, most restoration projects aim to mimic and accelerate this natural process (Dobson *et al.*, 1997; Palmer *et al.*, 1997; Walker *et al.*, 2007), maximizing efficiency and minimizing human input, and therefore minimizing the cost of restoration projects (Hardwick *et al.*, 2004; Chazdon, 2008). In this section, I do not aim to review exhaustively the techniques of ecological restoration of tropical forests but rather to present an overview of the most common ones and to show how ecological restoration can benefit from knowledge acquired by the study of natural succession.

There are a range of restoration techniques requiring different levels of input from the practitioner (Chazdon, 2008; Griscom & Ashton, 2011). Passive restoration, also called "unassisted restoration", requires no human intervention besides the removal of activities causing degradation (*e.g.* human-induced fire, grazing) (Holl & Aide, 2011; Zahawi *et al.*, 2014). Such a technique is effective, and sometimes better than more active intervention, in cases where there is no major barrier to the arrival and successful establishment of forest tree species (Sampaio *et al.*, 2007; Holl, 2012). In other cases, a variety of active restoration techniques can be used to alleviate these barriers: for example, perches placed in the restoration site can attract birds and hence

increase seed inputs (Shiels & Walker, 2003; Graham & Page, 2012), and removing grass can reduce competition and favour seedling establishment (Hardwick *et al.*, 1997; Cabin *et al.*, 2002a). These techniques are often referred to as "assisted natural regeneration" or "accelerating natural regeneration" (Hardwick *et al.*, 1997; Shono *et al.*, 2007). The introduction of woody species' individuals, as seed in the case of direct seeding or as planted seedlings, is necessary when the arrival of propagules is low or absent, but can also be used to accelerate succession or to introduce desired species that are missing (Griscom & Ashton, 2011). Observational and experimental studies carried out in natural forests can improve our understanding of the mechanisms and factors influencing degradation and succession (Figure 1) and provide insight into site-specific opportunities as well as constraints to restoration in order to select the most appropriate and cost-effective technique (Chazdon, 2008; Holl & Aide, 2011).

There are two main restoration techniques based on the plantation approach. Planting evenly-spaced seedlings across the whole site, in monoculture or mixed stands, is the classical method (Lugo, 1997; Parrotta *et al.*, 1997). The more recent applied-nucleation technique is gaining momentum as it offers a reduced-cost alternative. It is based on planting small patches of trees that then act as regeneration nuclei. With time, these nuclei expand and eventually coalesce, forming a continuous and heterogeneous tree cover (Holl *et al.*, 2010; Reis *et al.*, 2010; Corbin & Holl, 2012; Zahawi *et al.*, 2013). Applied nucleation and other restoration planting methods aiming to foster the establishment of other species besides the planted ones are based on application of the nurse plant effect (described in section 1.3.2): planted trees improve seed deposition, reduce grass competition and provide suitable microclimatic conditions for the arrival and establishment of other woody plants (Parrotta *et al.*, 1997; Hardwick *et al.*, 2004; Griscom & Ashton, 2011; Holl, 2012). These techniques therefore rely on the availability of propagules dispersed from the surroundings of the restoration site (Florentine & Westbrooke, 2004; Holl, 2012). The choice of species used for restoration planting and applied nucleation is, however, important because this choice influences the subsequent generations of trees that establish and therefore the long-term outcome of restoration (Parrotta, 1995; Murcia, 1997; Padilla & Pugnaire, 2006). In some cases, there is a risk of competition between planted trees and newly establishing ones that can slow down succession (Padilla & Pugnaire, 2006; Sampaio *et al.*, 2007).

Although planting a monoculture of exotic species has been used for restoration (Lugo, 1997; Feyera *et al.*, 2002), the use of a mixture of native species is increasingly preferred (Chazdon, 2003; Griscom & Ashton, 2011;

Holl, 2012). This technique requires a good knowledge of the ecology of these species for which the study of forest undergoing natural succession can be valuable. The "framework species" method aims to identify a set of suitable species for restoration planting based on their establishment success in open areas and capacity to quickly form a canopy, attract animal dispersers and provide suitable microclimatic conditions for the establishment of other species (Elliott *et al.*, 2003; Holtz & Placci, 2005). A functional trait-based approach can be useful to narrow down the list of candidate species by helping predict their performance and informing on other desired characteristics to meet restoration objectives (Martínez-Garza *et al.*, 2005; Martinez-Garza *et al.*, 2013; Ostertag *et al.*, 2015). Intraspecific variation of traits can also be useful to assess the potential plasticity of a species in response to a variety of environmental conditions (Martínez-Garza *et al.*, 2005).

2 Objectives

The overall objective of my research is to contribute field-based knowledge to advance ecological theories of secondary succession in tropical dry forests. I especially focus on (1) the models and long-term trajectories of succession and their drivers (papers II and IV) and (2) the underlying mechanisms and processes (papers I, III and study of seed fate). Each study considers a subset of the overall framework (Figure 1) by focussing on a restricted spatial and temporal scale (Figures 3 to 7). By providing information on the opportunities and barriers to natural succession, my results can have applications for science-based ecological restoration practices. The specific objectives are the following:

Identify the mechanisms by which established trees influence the establishment of woody plants leading to later stages of succession

Paper I focuses on the community and individual scales. It aims to identify the mechanisms of positive and negative plant-plant interactions between adult trees and each stage of the regeneration of young woody plants during secondary succession (Figure 3). The methodological approach of this study is the systematic review of observational and experimental studies. Understanding of these mechanisms has application for the use of the nurse plant effect in ecological restoration.
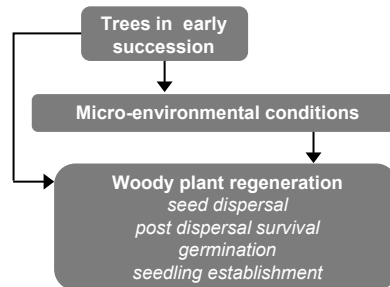

Figure 3. Conceptual framework of paper I.

Assess the resilience capacity of tropical dry forest tree and shrub communities and identify the factors affecting their degree of resilience

Paper II considers the long-term trajectories of succession. It uses a meta-analysis approach to assess the resilience capacity of taxonomic diversity and composition of tree and shrub communities in successional tropical dry forests (Figure 4). It also tests if regional abiotic environmental factors (precipitation regime and water availability) and land use history of the site influence the rate and directionality of changes in taxonomic diversity and composition. The results can help to identify the opportunities and barriers to restoration of the diversity of tropical dry forests and guide the choice of restoration strategies (passive *versus* active restoration).
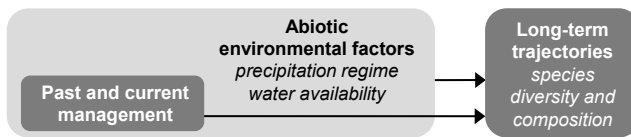
Figure 4. Conceptual framework of paper II.

Identify the factors structuring woody plant assemblages under isolated pasture trees

Paper III considers the first stage of secondary succession in pasture sites. The aim is to test the importance of landscape factors and attributes of isolated trees in explaining the properties of the woody plant regeneration assemblages beneath their crowns (Figure 5). Both the taxonomic and functional compositions of
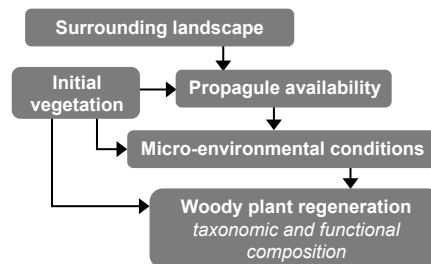
Figure 5. Conceptual framework of paper III.

the regeneration assemblage are considered. The methodological approach is survey of the woody vegetation regenerating under a large sample of pasture trees. The results can inform practitioners about the factors to consider when selecting species to plant to initiate restoration (or which trees to prioritise for protection within pasture), especially when using the technique of applied nucleation.

Identify the direction and drivers of change in functional composition of sapling communities during succession

Paper IV considers the long-term trajectories of succession at the scale of the tree community. It uses a functional trait-based approach and assesses the

relative contribution of species turnover and intraspecific variation to the response of community-level trait values to changes in environmental conditions (Figure 6). The methodological approach is measurement of leaf functional traits of all saplings in plots of two chronosequences. The results of this study can inform on the values of functional traits associated with different stages of succession.
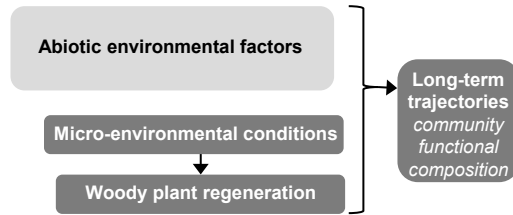
Figure 6. Conceptual framework of paper IV.

Assess the influence of the changing abiotic and biotic environmental conditions during secondary succession on the fate of tree seeds and identify the underlying mechanisms

The study of seed fate addresses one of the research gaps identified by Paper I. It focuses on the community and individual scales and considers an open pasture area, and young and intermediate-aged secondary forests. It uses an experimental approach to test the relative influence of shading by tree canopies and leaf litter as factors determining the fate of seeds (removal by predators and germination) artificially dispersed into the sites (Figure 7). The results will provide information on the potential of restoration by direct sowing.
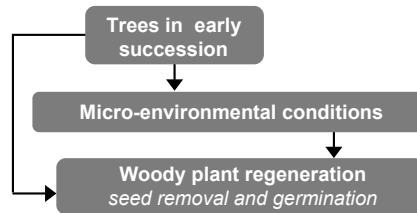
Figure 7. Conceptual framework of the study of seed fate.

3   Material and methods

3.1   Study area and study sites

Three of the studies (papers III and IV and the study of seed fate) were based on field data that I collected in, or in the surroundings of, the *Área de Conservación de Guanacaste* (ACG) (ACG, 2016), in the north-west of Costa Rica (Figure 8). This area has been extensively used for agriculture (mainly cattle farming, and sugar cane and cotton cultivation) and wood extraction since the Spanish conquest in the early 1500s, which led to the clearing of most of the forested area by the 1970s. This trend started to reverse in the 1980s as a result of the combination of conservation policies and changes in economic activities (Calvo-Alvarado *et al.*, 2009). In the mid-1980s, an ambitious restoration project started at the instigation of Dr Daniel Janzen (Janzen, 2002; Aronson *et al.*, 2005). This project is mainly based on fostering the natural re-establishment of the forest by alleviating the main barriers to forest regeneration through the purchase of degraded agricultural land, the exclusion of cattle and the control of anthropogenic fires (Janzen, 2002). Originally centred around the 10 000 ha of tropical dry forests of the Santa Rosa National Park, the conservation area has gradually extended to reach the current 163 000 ha of protected area comprising marine, tropical dry forest, cloud forest and rain forest habitats (ACG, 2016).
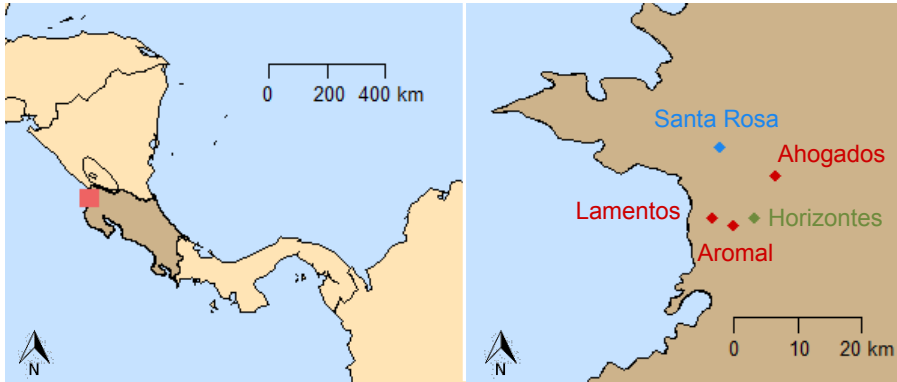
Figure 8. Study area and study sites. The red square on the map on the left indicates the area enlarged on the right. The map on the right shows the study sites: red for paper III, blue for paper IV and green for the study of seed fate.

The study area is at the wet end of the rainfall gradient of tropical dry forests, with ~ 1640 mm mean annual precipitation (data from the meteorological station of Liberia 10.58°N; 85.53°W collected between 1958 and 2014, Instituto Meteorológico Nacional de Costa Rica, 2016). The climate is characterised by strong seasonality of precipitation with a 5-6 month dry season and more than 95% of the mean annual precipitation falling during the May-November wet season (Figure 9). Mean temperatures vary little over the year and have an annual mean of 27.5 °C (data from the meteorological station of Liberia collected between 1977 and 2014, Instituto Meteorológico Nacional de Costa Rica, 2016). Maximum temperatures can exceed 40 °C (personal measurement).
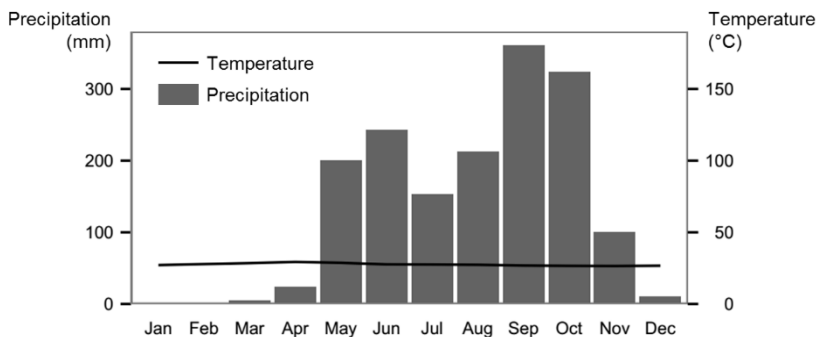
Figure 9. Climate diagram of the study area. Data *Instituto Meteorológico Nacional de Costa Rica*, meteorological station of Liberia 10.58°N; 85.53°W. Precipitation 1958-2014, temperature 1977-2014 (Instituto Meteorológico Nacional de Costa Rica, 2016).

The landscape is a mosaic of pastures and secondary forests of different ages, resulting from the history of land use. The natural vegetation is tropical dry forest (Holdridge *et al.*, 1971) formed by a mixture of evergreen trees and trees of diverse degrees of deciduousness (Borchert *et al.*, 2004). Janzen (2002) estimated that an old-growth forest in the area has 30-60% of its canopy space occupied by evergreen trees, while the proportion is higher in the understory. Woody lianas are abundant in successional forests but less so in the closed-canopy old-growth forests (Sanchez-Azofeifa *et al.*, 2009). In nearby tropical dry forest, Frankie *et al.* (1974) found that 30% of the species were anemochorous, which is a relatively low proportion when compared with other tropical dry forests (Vieira & Scariot, 2006b), and 50% of species had fleshy fruits.

The dry forests of Guanacaste host a high number of plant species. Janzen and Liesner (1980) listed almost 1000 species of plants, excluding grasses and non-vascular cryptogams, encountered in Guanacaste. Gillespie *et al.* (2000) found an average of 12 species of trees and shrubs and 4.5 species of lianas per 100 m^2 in Santa Rosa, making this the richest of the seven tropical dry forest sites that they studied in Nicaragua and Costa Rica, and one of the richest ones in the whole Neotropics. As in all Neotropical dry forests with the exception of the Caribbean and Florida, Leguminosae is the most species-rich family in Guanacaste (Gentry, 1995; Gillespie *et al.*, 2000; Pennington *et al.*, 2006; Pennington *et al.*, 2009). Bignoniaceae is the family represented by the most species of lianas (Gentry, 1995; Gillespie *et al.*, 2000). There is generally little overlap in species composition between these dry forests and the neighbouring moist forests (Murphy & Lugo, 1995). This floristic differentiation between tropical dry and wet forests is consistent with the finding of Dexter *et al.* (2015) that, within the Neotropics as in the other tropical areas, there is a clustering of floristic composition by vegetation type[7]. This trend indicates strong phylogenetic biome and niche conservatism, only lineages with adaptations enabling survival of drought being able to establish in tropical dry forests (Hughes *et al.*, 2013). However, Gentry (1995) reported the occurrence of moist forests plants, such as species in the genera *Ficus* and *Psychotria*, in the tropical dry forests of Guanacaste, which he attributed to the presence of moister gallery forests in the dry forest landscape. At the continental scale, the tropical dry forests of Costa Rica have floristic affinities with a wide range of tropical dry forests including those in Mexico and Central America, the Caribbean and the Northern part of South America (Colombia and Venezuela), with different classifications showing stronger affinities with one or the other of these floras (Linares-Palomino *et al.*, 2003; Linares-Palomino *et al.*, 2011).

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[7] *N.B.* At the global scale, however, the clustering by continent is stronger.

The affinities of floristic composition between these areas results from the dispersal opportunities provided by the land bridge of the Panama Isthmus since its closure ~3 million years ago, but also through island stepping stones before that (Murphy & Lugo, 1995; Linares-Palomino *et al.*, 2003; Bagley & Johnson, 2014).

Natural fires are extremely rare in Guanacaste (Hartshom, 1983). No fires caused by lightning have been observed during the dry season and natural fires are limited to those caused by volcanic activity (Janzen, 2002). As a consequence, there are no natural savannas in Guanacaste, and there is no evidence for the presence of savannas in the past (Janzen, 2002). On the other hand, anthropogenic fires are frequent and fostered by the presence of fire-prone exotic grasses such as *Hyparrhenia rufa* in pasture sites (Daubenmire, 1972; Janzen, 2002). They are a major barrier to forest regeneration in the early stage of succession and their control is therefore a key factor in the success of the restoration of the dry forest in Guanacaste (Janzen, 2002).

For paper III, I worked in three active pasture sites located in private land (Ahogados 10.80°N, 85.54°W, Lamentos 10.74°N, 85.63°W and Aromal 10.73°N, 85.60°W). For paper IV, I collected data in Santa Rosa (10.84°N, 85.62°W), in plots in successional forests located to span two chronosequences in each of two distinct forest types (oak dominated forests and forests with a more even mixture of species). For the study of seed fate, I worked in an open area and two successional forests in the Experimental Forest Station of Horizontes (10.74°N, 85.57°W) (Figure 8).

3.2   Data acquisition

3.2.1 Systematic review of the literature

For papers I and II, I used data and observations from previously published studies. To increase objectivity, comprehensiveness and repeatability, I followed a systematic protocol to search for and select studies (Pullin & Stewart, 2006; Woodcock *et al.*, 2014). I searched at least two databases of scientific literature using an explicit search string. I then selected the studies following clearly reported inclusion criteria.

3.2.2 Observational approach: vegetation survey

Papers II, III and IV use an observational approach based on vegetation surveys to study changes occurring during succession at the scale of whole tree communities.

Paper II: species diversity and composition

For paper II, I used raw data provided by the authors of the included studies in the form of floristic tables of species abundance for plots at different successional ages. The tree community of each plot was characterised in terms of species richness, species evenness and similarity of species composition with the composition of old-growth forests.

To calculate species richness, I used the standardisation method proposed by Colwell *et al.* (2012) to account for differences in stem density among plots. I used the individual-based approach, as I had one sample for each community (*i.e.* plot), with multinomial model to be able to standardise the species richness to a chosen number of individuals (15 in this case). When the actual number of individuals in the plot was less than 15, the species richness was obtained by rarefaction (interpolation) and when it was greater than 15, the species richness was obtained by extrapolation. Combining the two methods was not a problem because the interpolation and extrapolation curves joined smoothly (Colwell et al. 2012). I chose to standardise the richness to a number of 15 individuals because 15 was less than three times the actual number of individuals in 98.5% of the plots; Colwell et al. (2012) specifically warn against extrapolating to a number of individuals that is more than three times the actual number. I used the function *iNEXT* of the package *iNEXT* (Hsieh *et al.*, 2015) in R (R core team, 2015) to calculate species richness.

To calculate species evenness, I used two of the most common evenness indices, Shannon and Simpson (Magurran, 2005). Both are based on a corresponding measures of species diversity, the Shannon and Simpson diversity indices, respectively (Maurer & McGill, 2011) and differ is their approach and properties (Smith & Wilson, 1996; Magurran, 2005; Jost, 2010). They notably differ in their dependency on species richness, the Shannon index being dependent while the Simpson index is not (Jost, 2010). Both indices were calculated using the function *diversity* in the package *vegan* (Oksanen *et al.*, 2015) in R.

To calculate the similarity of species composition in each successional plot with the composition of old-growth forests, I calculated two similarity indices, the Sørensen and Chao-Sørensen indices, for each pair of successional and old-growth forest plots of each study (Chao *et al.*, 2005). When a study considered several old-growth plots, I averaged the similarity across old-growth forest plots for each successional plot. The Sørensen index is an occurrence-based index: it compares the number of shared species to the mean number of species in a single plot (Jost *et al.*, 2011). For this reason, it gives a more local perspective than the Jaccard index, which compares the number of shared species to the number of species in the combined two plots. I calculated the

Sørensen index using the function *betadiver* in the package *vegan* (Oksanen *et al.*, 2015) in R. The Chao-Sørensen index is an abundance-based index: it assesses the probability that two randomly chosen individuals (one in each plot considered) belong to one of the species shared between the two plots. I calculated this index using my own function in R.

I had two reasons for considering two indices. (1) While the occurrence-based Sørensen index allowed me to assess the recovery of a list of species during succession, the abundance-based Chao-Sørensen index allowed me to assess the recovery of the hierarchy of species (*i.e.* their relative abundance). The two indices give different information that can be applied respectively to restoration activities with different objectives. (2) Because the Chao-Sørensen index assesses the probability that two randomly chosen individuals belong to a shared species, if the shared species are abundant (or rare) in one or both plots, their probability to be randomly chosen will be higher (or respectively lower) so the index is expected to be higher (or respectively lower). On the other hand, the occurrence-based Sørensen index will not change. I therefore considered that the Chao-Sørensen index gives more weight to the common species. I acknowledge that another solution to study the difference in the recovery of common and rare species could have been to use the Horn and the Morisita-Horn indices, two abundance-based similarity indices giving more weight to the rare and common species, respectively (Jost *et al.*, 2011). I have chosen not to use the Bray-Curtis index, which is another commonly used abundance-based index of similarity, because it is very sensitive to large differences in the number of individuals between the plots considered (Jost *et al.*, 2011), which was likely to happen with the successional data that I studied.

Paper III: species and functional compositions
For paper III, I surveyed the woody vegetation regenerating under the crown of 90 isolated trees in pasture. I characterised these regeneration assemblages in terms of the number of individuals, number of species and functional composition. For the functional composition, I considered categorical functional traits (life form, dispersal syndrome[8], leaf phenological habit, leaf compoundness and membership of the Leguminosae family) based on literature and on-line resources. I also characterized the isolated trees by their position in the landscape relative to nearby tree patches (in terms of distance and area of tree patches in buffers ranging from 100 to 1000 m around the focal isolated tree), using orthophotos analysed in ArcGIS. I also considered structural

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[8] For seed dispersal type, I considered two categories (zoochorous *versus* anemochorous and autochorous). For zoochorous species, the data available did not allow me to distinguish accurately between the different types of animal dispersers.

variables (*e.g.* height, crown area) and functional traits (seed dispersal type, leaf phenological habit and ability to fix nitrogen) of the isolated trees.

Paper IV: community functional composition

For paper IV, I surveyed all saplings present in 12 plots (5 x 50 m) located in forest of different successional ages. For each sapling, I measured the following leaf functional traits using standard protocols (Cornelissen *et al.*, 2003; Perez-Harguindeguy *et al.*, 2013):

> ➤ traits associated with resource economics strategies: specific leaf area (SLA), leaf density, leaf area (LA), leaf dry matter content (LDMC), petiole length, leaf thickness, and leaf nitrogen (LNC), phosphorous (LPC) and carbon concentration (LCC),
> ➤ traits associated with dry and hot conditions: leaf compoundness, leaf pubescence, leaf phenological habit, leaf density and LDMC,
> ➤ stoichiometric ratios: C/N and N/P,
> ➤ membership of the Leguminosae family.

I then calculated two types of trait community mean values: (a) the specific mean using a trait value *per species* and *per plot* and therefore taking into account intraspecific variation of trait values and (b) the fixed mean using a mean trait value *per species* calculated *across plots* and therefore ignoring intraspecific variation (Lepš *et al.*, 2011).

3.2.3 Experimental approach

For the study of seed fate, I used an experimental approach to test the influence of tree cover in secondary forest on the fate of seeds dispersed underneath. I used a fully factorial design with four factors (four replicates for each combination of factors and 20 seeds per replicate) (Figure 10):

> ➤ site: two forest sites of different successional ages (14 and 30 years old) and an open area,
> ➤ litter treatment: naturally accumulating litter and litter removal,
> ➤ predation treatment: with or without wire mesh protection against predation (holes in mesh are 1.27 x 1.27 cm),
> ➤ species of seeds.
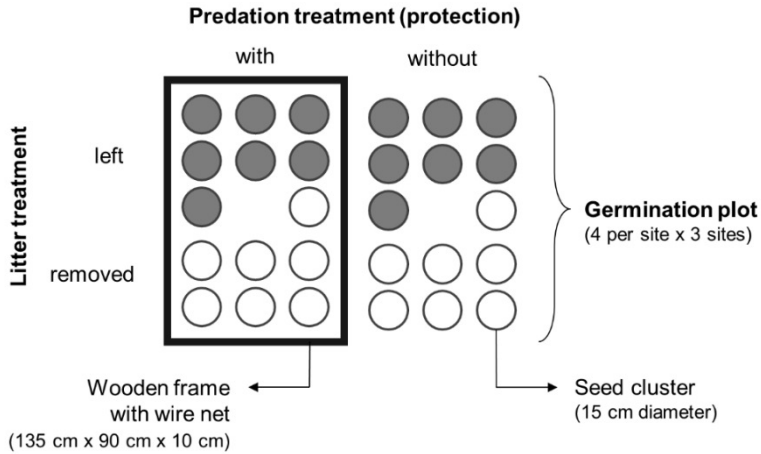
Figure 10. Experimental design for the study of seed fate. Each seed cluster contains 20 seeds of a given species. All depots of a same germination plot have a different combination of species, litter and predation treatments.

I tested seven species that are common in the tropical dry forests of Guanacaste, have contrasting seed traits (seed dispersal type, size and shape) and belong to different families (though two species of the common Leguminosae family were tested) (Figure 11).

Figure 11. Seeds of the seven species tested in the study of seed fate. The approximate length of *Simarouba amara* seeds is 2 cm. Photos Géraldine Derroire.

For each seed cluster, I monitored, every two weeks over 12 weeks, the proportion of seeds having one of the following fates:

➢ germination,
➢ removal (seed no longer present in the cluster),
➢ pathogen attack or predation *in situ*.

3.2.4 Environmental conditions

For paper II, I considered several environmental factors at the regional and site scales for each reviewed study. I tested their influence on the direction and rate of change in species diversity and composition during succession. These factors were:

➢ the former land use of the site before the forest started to re-establish,
➢ the precipitation regime (mean annual precipitation and number of dry months),
➢ the availability of water (measured as the ratio between annual potential evapotranspiration and mean annual precipitation).

For paper IV and the study of seed fate, I measured a set of microclimatic factors expected to change during succession (those followed by an asterisk were considered only for the study of seed fate): air temperature (logged over several days), soil temperature* (repeated measurements at different times), canopy openness (measured using hemispherical photographs), red/far red light ratio* (repeated measurements at different times), air humidity (repeated measurements at different times) and soil moisture (repeated measurements at different times. For paper IV the measurements were taken by Bonnie Waring). For paper IV, I also considered soil physical and chemical factors (data collected by Powers *et al.*, 2009) that I assumed were not influenced by changes occurring during succession, to assess possible bias (caused by indirect relationships between the variables of interest due to their correlation with site environment), which is an inherent risk of the chronosequence approach.

3.3   Data analysis

3.3.1 Meta-analysis

For the meta-analysis conducted in paper II, I used statistical methods adapted to summarize the results of several studies. Meta-analyses allow the calculation of an overall effect size (in my study, rates of change in species diversity and composition indices). They combine the effect sizes calculated for each study while accounting for their unequal precision, by weighting them by their variance (Koricheva & Gurevitch, 2013). To explain the heterogeneity between

studies, I then carried out meta-regressions, a type of meta-analysis enabling to test the effect of covariates (also called moderators, in my study the duration of succession studied, the previous land use, the rainfall regime and water availability) on the magnitude of effect size to be tested (Mengersen *et al.*, 2013). All analyses were performed using the package *Metafor* (Viechtbauer, 2010) in R.

For paper I, it was impossible to conduct a meta-analysis because of the low number of studies meeting the inclusion criteria, the heterogeneity of their methodological approaches and the absence of reporting of the variance of the results in most cases.

3.3.2 Ordination

I used ordination methods for the variables that were multivariate (taxonomic composition for paper III and functional trait association for paper IV).

For paper III, I tested the effect of the attributes of isolated trees on the taxonomic composition of the regeneration assemblages using redundancy analysis (RDA). This is a canonical ordination technique that combines regression and principal component analysis (PCA) (Borcard *et al.*, 2011). It computes axes that best explain the variation of the response variable and expresses each axis as a linear combination of the explanatory variables (Legendre & Gallagher, 2001). I carried out a forward model selection procedure to identify the model with the best sets of explanatory variables (Borcard *et al.*, 2011).

For paper IV, I used the RLQ method to understand the relationship between environmental factors and functional traits. In this analysis, functional traits were considered together (a multi-trait approach) to understand plant strategies and trade-offs. RLQ is an ordination technique analysing the matrices of species distribution across plots, environmental factors of plots and species/individuals traits to find axes that maximize the squared cross-variance of linear combinations of environmental factors and traits (Dray *et al.*, 2014). The resulting coefficients were then presented graphically. I used two partial RLQs (Wesuls *et al.*, 2012), performed with the package *Ade4* (Dray & Dufour, 2007) in R, to separate the part of the trait-environment relationship that was due to intraspecific variation of trait values from these due to species turnover.

3.3.3 Regression

I used regression models (linear model, generalised linear models (GLM) or mixed-effects models, depending on the distribution of the response variable and the necessity to include a random factor), to test:

> the effect of the precipitation regime on the importance of positive and negative effects of established trees on regeneration (paper I),
> the influence of landscape factors and attributes of isolated trees on properties of the regeneration assemblage under their crowns (paper III),
> the effect of experimental treatments on the proportion of seed showing each recorded fate (study of seed fate),
> the changes in trait values with ontogeny and the effect of environmental factors on community weighted mean values for each functional trait separately (single-trait approach) (paper IV). I expressed the sum of squares obtained by linear regression of each community value with one or the other of the two types of community weighted means presented in section 3.2.1 as a percentage of the total sum of squares to get the contribution of species turnover and intraspecific variation to the response of communities to environmental factors, following the method of Lepš *et al.* (2011) and using the function *trait.flex.anova* that they coded for R (Lepš *et al.*, 2011).

Table 1 presents a summary of the methods used for each study.

Table 1. *Overview of methods.*

Study	Study sites	Methodological approach		Data analysis
Paper I	Tropical dry forests across the world	Review	-	Narrative review, regression
Paper II	Tropical dry forests across the world	Review	Taxonomic	Meta-analysis
Paper III	Pasture sites (Ahogados, Aromal, Lamentos; Costa Rica)	Observational	Taxonomic and trait-based	Ordination, regression
Paper IV	Successional forests (Santa Rosa; Costa Rica)	Observational	Trait-based	Ordination, regression
Study of seed fate	Open site and successional forests (Horizontes; Costa Rica)	Experimental	Taxonomic	Regression

4 Main results and specific discussion

4.1 Effects of established trees on woody regeneration

This section presents and discusses the main results of paper I.

4.1.1 Positive *versus* negative interactions at each stage of regeneration

The reviewed studies showed the importance of the effects of trees establishing in the early stages of secondary succession on the subsequent regeneration of woody species. Observational studies provided support for potential net effects while experimental studies enabled understanding of the mechanisms underlying these effects. I discuss below the type of effect (positive or negative) and the possible underlying mechanisms for each stage of the process of regeneration: seed dispersal, survival of seeds, germination and seedling establishment, and I summarize them in Figure 12.

Effects on seed dispersal

The five studies researching the effects of established trees on seed dispersal showed an overall positive effect of the presence of trees. This effect is mediated by animal dispersers that are attracted by established trees (Vieira & Scariot, 2006b), resulting in a higher proportion of zoochorous species under tree canopies (Wydhayagarn *et al.*, 2009) and an increase in this proportion with succession (Opler *et al.*, 1980a).

Effects on post-dispersal survival of seeds

The three studies researching the effects of established trees on post-dispersal seed survival suggested that there can be both a positive direct effect, the canopy cover mitigating the conditions responsible for seed desiccation (Vieira & Scariot, 2006a), and an indirect effect mediated by seed predators. For the latter, there was evidence of both a decrease (Hammond, 1995) and an increase (Wassie *et al.*, 2010) in seed predation and removal under closed canopies.

Overall, the effect on post-dispersal seed survival is complex as it depends on the type of seed, the type of consumer and the successional stage. More studies, especially experiments, are needed to get a better understanding of these effects.

Effects on seed germination

Hardwick *et al.* (1997) found a higher germination rate under forest cover than in open areas, supporting a positive effect of established trees on seed germination. Experimental studies manipulating shading and watering suggest that this effect occurs via increased moisture conditions under tree cover (Hardwick *et al.*, 1997; McLaren and McDonald, 2003a; but compare Ray and Brown, 1995). However, the response of seed germination was species-specific (Hardwick *et al.*, 1997) and further studies are needed to identify the seed traits explaining the difference in species' responses.

Effects on seedling establishment

The reviewed studies suggested a positive effect of established trees on seedling survival, mediated by mitigation of desiccating conditions during the dry season, and an overall negative effect on seedling growth through limitation of light during the wet season (Cabin *et al.*, 2002a; McLaren & McDonald, 2003b; Wolfe & Van Bloem, 2012). However, the effects on seedling growth are complex: they depend on the successional stage (Hammond, 1995), the leaf phenology of both the established trees (Gerhardt, 1996) and the seedlings (Ray & Brown, 1995) and can be altered by changes in resource allocation by the seedlings in response to environmental variation (Rincón & Huante, 1993).
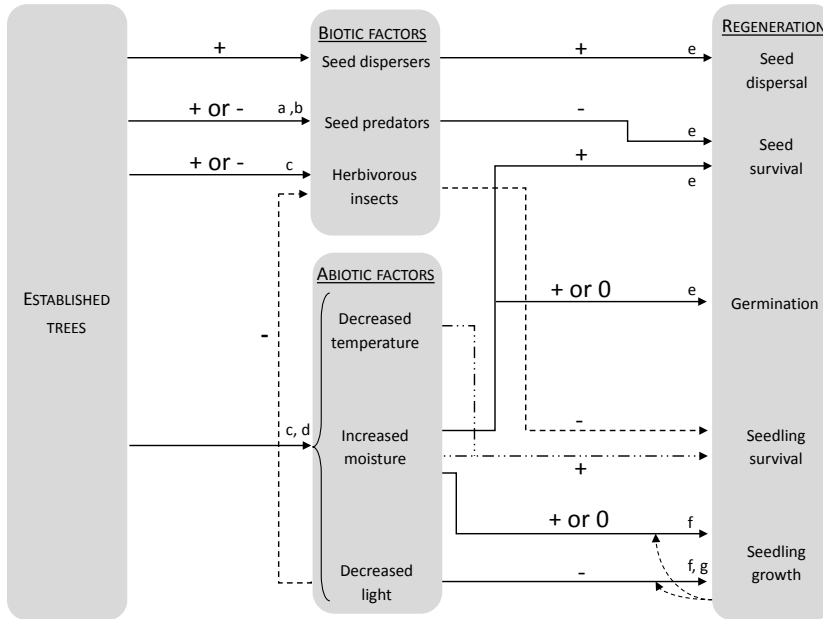
Figure 12. Mechanisms underlying the effect of trees that establish in the early stages of secondary succession on subsequent regeneration of woody plants in tropical dry forests. The plus, minus and zero symbols indicate positive, negative, and absence of effect, respectively. The letters on the arrows refer to the factors influencing the effect considered: (a) successional stage, (b) predator type, (c) leaf phenology of the established tree species, (d) density of canopy cover, (e) seed type, (f) regenerating species, and (g) intensity of shading.

4.1.2 Support for the stress gradient hypothesis

I used logistic regressions to assess the probability that a study would show evidence for a net positive/negative effect of established trees on regeneration as a function of the mean annual rainfall. I found that the probability of a positive effect on seedling survival decreased with increasing rainfall, while the probability of a negative effect increased (Figure 13). This result supports the stress gradient hypothesis, which predicts that facilitation is more important when environmental conditions are particularly harsh (Bertness & Callaway, 1994; Callaway, 1995; Callaway & Walker, 1997). However, my analysis did not support this hypothesis for seedling growth (p = 0.853 for net positive effect and p = 0.862 for net negative effect). These results are based on a relatively low number of studies; it would therefore be interesting to conduct these analyses again once more studies become available. The low number of studies for the other regeneration stages prevented the stress gradient hypothesis being tested for them.
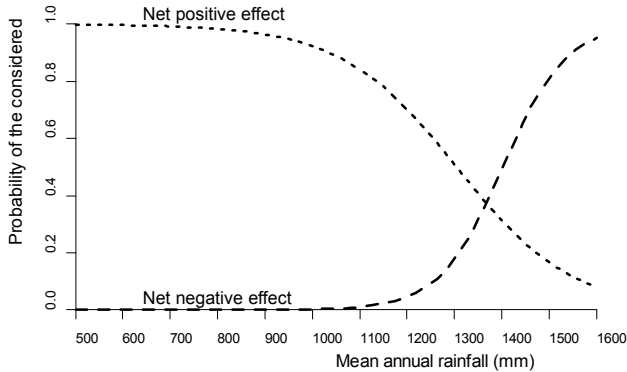
Figure 13. Probability of observing a net positive effect or a net negative effect of established trees on seedling survival as a function of the mean annual rainfall. Models fitted with logistic regressions: positive effect (p = 0.008, R^2 = 0.43), negative effect (p=0.009, R^2 = 0.56).

4.2   Changes in species diversity and composition during succession

This section presents and discusses the main results of paper II.

4.2.1 Resilience of species richness and convergence of species composition

Using meta-analysis of studies of the taxonomic changes occurring during succession in tropical dry forest, I found a positive rate of change (the effect size shown by the meta-analysis) in standardised species richness with increasing successional age (Figure 14). This result shows a gradual accumulation of species that is consistent with the trends generally observed in tropical forests (Chazdon *et al.*, 2007; Letcher & Chazdon, 2009; Dent *et al.*, 2013). For the studies that included data for old-growth forests, species richness reached a level similar to that of old-growth forests in 60 years or less, which is consistent with the results of Martin *et al.* (2013) across tropical forests.

Interestingly, the results for evenness obtained with the Shannon evenness and the Simpson evenness indices differed: Shannon evenness index showed an overall significant increase with succession, whereas no significant trend was observed for Simpson evenness index. This difference might be due to the divergence in conceptual opinions about what evenness actually is, as reflected in the differences in the way it is calculated between the two indices (Tuomisto, 2012). While the Simpson evenness index is independent of species richness, the Shannon evenness index is not (Smith & Wilson, 1996; Magurran, 2005; Jost, 2010; Tuomisto, 2012). The trend observed for the

Shannon evenness index with succession might therefore result from the trend observed for species richness.

The similarity of species composition with old-growth forests was found to increase with successional age in two separate analyses of the short- and long-duration studies (Figure 14). However, the rate of change was slow and the similarity of successional forests with old-growth forests remained relatively low even after several decades. This result suggests that, although the species composition of secondary forests converges towards that of old-growth forests, there is substantial uncertainty about the recovery of species composition. The recovery of the exact composition of old-growth forests may never happen (Chazdon *et al.*, 2007). However, the low levels of similarity of successional plots with old-growth forests should be interpreted with caution. The size of the sampling area is likely to be too small to encompass all species present in the studied communities, as shown by the fact that for most of the plots, the species accumulation curves do not reach a level value. Part of the dissimilarity between plots could therefore be due to species that are present in the whole communities but not in the plots. There are two possible solutions to this problem. (1) At the data collection stage, the plot size could have been chosen to be large enough to encompass the majority of the species present in the community (as indicated by a levelling of the species accumulation curves). Because I used secondary data for this meta-analysis, this solution was impossible for me to implement. (2) During the data analysis, I could have used a method for estimating the similarity that takes into account the unseen species, such as the abundance-based Chao-Sørensen estimator (Chao *et al.*, 2005). However, the reason why I did not use this index is because there is no occurrence-based equivalent, to the best of my knowledge. Another result that needs to be interpreted with caution is the difference in rates of change of similarity indices for studies of different durations. There is only one study for the shorter duration and the higher rate of change for this study may be idiosyncratic.

Overall, my results show sufficient resilience of species richness to support the potential of secondary forests for long-term biodiversity conservation. Nonetheless, active restoration intervention may still be needed to recover the species composition of old-growth forests.
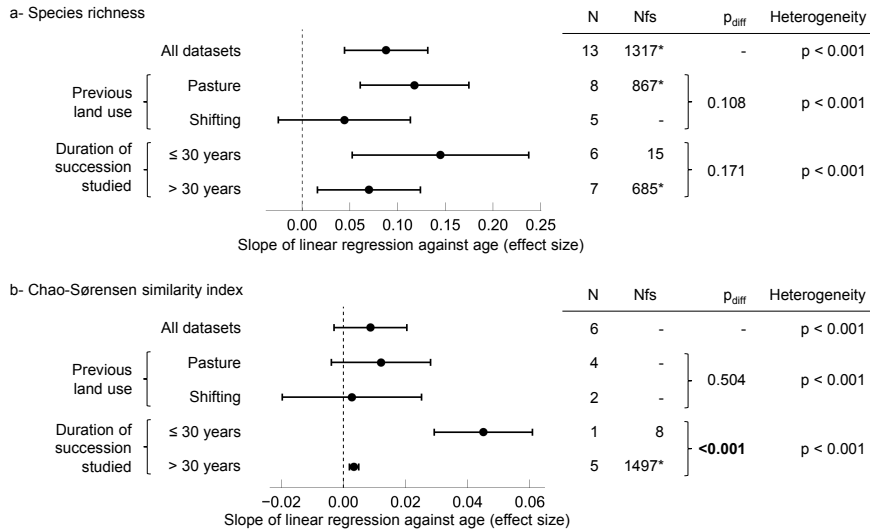
a- Species richness

		N	Nfs	p_{diff}	Heterogeneity
All datasets		13	1317*	-	p < 0.001
Previous land use	Pasture	8	867*	0.108	p < 0.001
	Shifting	5	-		p < 0.001
Duration of succession studied	≤ 30 years	6	15	0.171	p < 0.001
	> 30 years	7	685*		p < 0.001

b- Chao-Sørensen similarity index

		N	Nfs	p_{diff}	Heterogeneity
All datasets		6	-	-	p < 0.001
Previous land use	Pasture	4	-	0.504	p < 0.001
	Shifting	2	-		p < 0.001
Duration of succession studied	≤ 30 years	1	8	**<0.001**	p < 0.001
	> 30 years	5	1497*		p < 0.001

Figure 14. Estimated effect sizes (slope of the linear regression against successional age) of one meta-analysis (all datasets) and two meta-regressions (with previous land use and duration of succession studies) for a) species richness (standardised to 15 individuals) and b) the Chao-Sørensen species composition similarity with old-growth forests. The error bars indicate the 95% confidence intervals. N is the number of datasets for each case. Nfs is the fail-safe number (*i.e.* the number of datasets with null effect that need to be added to lose the significance of the estimated effect size at p = 0.05) for the significant effect sizes. The estimate is robust if Nfs > 5N+10 (indicated with an asterix). p_{diff} is the p-value for the significance of the difference between two modalities of a moderator. Heterogeneity between datasets is tested with the Cochran's Q test for meta-analysis and with the Q-E test for meta-regressions (a significant p-value indicates heterogeneity). Shifting means shifting cultivation.

4.2.2 Factors affecting the rates of changes

I expected a difference between pasture and shifting cultivation land uses in their influence on subsequent succession because of their different effects on the soil and remnant vegetation. However, I did not find any significant differences in the rates of change for the analysed indices between the two previous land uses (except for Shannon evenness index). Similarly, Norden *et al.* (2015) and Poorter *et al.* (2016) did not find any effects of previous land use on changes in forest structure and species density with succession. This absence of correlation can be explained by the heterogeneity within the two land use categories due to differences in the abundance of remnant vegetation, the intensity and duration of the land use, the use of fire and the post-abandonment disturbance regime.

The precipitation regime (mean annual precipitation and number of dry months) and the availability of water (ratio between annual potential evapotranspiration and mean annual precipitation) had no significant effect on

the rate of change in the analysed indices. A possible reason is that these variables can have opposite effects on the importance of resprouting and facilitation (Callaway & Walker, 1997; McDonald *et al.*, 2010) and on the size of the species pool capable of tolerating low levels of water availability.

The absence of significant effects of the previous land-use, the precipitation regime and the availability of water should, however, be interpreted with caution because of the low number of studies included in the meta-analyses. It will be useful to conduct these analyses on a larger dataset, once more studies become available.

The heterogeneity of rate of change in species diversity and composition observed could be explained by factors that could not be tested in my meta-analysis, such as the position of successional forests in the landscape (Castillo-Nunez *et al.*, 2011; Chazdon, 2014; Arroyo-Rodriguez *et al.*, 2016), differences in soil properties (Powers *et al.*, 2009) and stochastic events (Norden *et al.*, 2015).

4.3   Isolated trees as nuclei of regeneration in pasture

This section presents and discusses the main results of paper III.

4.3.1 Effect of the surrounding landscape

Most of the properties of the regeneration assemblages below the crowns of isolated trees in pastureland (number of individuals, number of species and functional composition, but not life form) were correlated with at least one of the landscape factors analysed (position of the tree in the landscape relative to patches of trees, measured as a distance and as the area of tree patches in buffers of radius from 100 to 1000 m). These results support the important influence of the surrounding landscape on the re-establishment of forest on agricultural land (Chazdon, 2014). However, the effect of the landscape varied greatly between study sites, suggesting the importance of other landscape factors, such as the wider abundance of scattered trees or live-fences acting as stepping stones and corridors for disperser animals (Estrada *et al.*, 1993; Chazdon *et al.*, 2011).

4.3.2 Effect of isolated trees

Isolated trees differed in their influence on the regeneration assemblage establishing beneath their crown: I found that the functional composition of the regeneration assemblage was clearly associated with the attributes of the isolated trees (Figure 15). However, these attributes only poorly explained the taxonomic composition of the regeneration assemblages, which was very site

dependent. These results support the existence of a more general determinism and predictability of successional trajectories when considered through functional composition rather than taxonomic composition, in line with the results of several other studies of succession (Fukami *et al.*, 2005; Alvarez-Anorve *et al.*, 2012; Muniz-Castro *et al.*, 2012; Swenson *et al.*, 2012; Dent *et al.*, 2013; Purschke *et al.*, 2013).

The influence of attributes of isolated trees on the functional composition of the regeneration assemblage beneath their crowns can be explained by two mechanisms:

➤ Amelioration of environmental conditions: there was a lower proportion of individuals having traits associated with tolerance of drought and heat (deciduous and compound-leaved) in the regeneration assemblage under trees able to cast more shade (wider crowns and evergreen leaf phenology). Increased shade leads to a decrease in air temperature and an increase in air humidity and soil moisture (Rhoades *et al.*, 1998; Callaway, 2007), allowing less drought-adapted species to establish.

➤ Attraction of seed dispersal agents: the analysis predicted that, excluding individuals conspecific with the tree above, 1.3 times more zoochorous individuals regenerate under a zoochorous tree than under an anemochorous tree. This result supports the importance of the seed dispersal type of a tree for its capacity to attract seed dispersers (Da Silva *et al.*, 1996; Galindo-González *et al.*, 2003; de la Peña-Domene *et al.*, 2014).
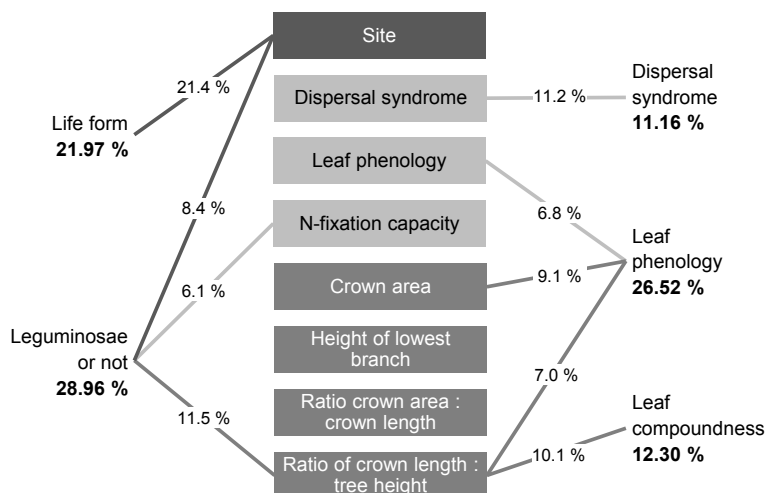

Figure 15. Relationships between the attributes of isolated trees and the functional composition of the assemblages of woody plants regenerating beneath their crowns. The lines indicate all the significant covariates kept in the best models (attributes of isolated trees, boxes in the centre) with

the response variable of these models (properties of the regeneration assemblage, on the sides). The percentage of deviance explained by each model is given in bold below each response variable and the percentage of deviance explained by each isolated tree attribute in a model is given on the line.

4.4 Community assembly during succession

This section presents and discusses the main results of paper IV.

4.4.1 Changes in functional composition with succession

Multi-trait and single-trait analytical approaches both showed directional changes during succession driven by the associated changes in environmental conditions (Figure 16). The changes followed two main trends, the first being by far the most important:

1. A shift from conservative towards acquisitive leaf strategies and a decrease in the proportion of legumes: this trend was associated with decreases in the canopy openness and air temperature measured during the wet season, which is the main growing season. In early succession, with high evaporative demand, conservative leaf-trait strategies reduce leaf heat and transpiration (Poorter & Markesteijn, 2008), while legumes maintain a high rate of resource acquisition through efficient water use (Reyes-Garcia *et al.*, 2012).

2. A decrease in drought-coping strategies (leaf deciduousness and pubescence): this trend was associated with the decreases in canopy openness and air temperature measured during the dry season, during which drought-coping strategies reduce mortality (Poorter & Markesteijn, 2008).

Interestingly, these trends are consistent with other studies carried out in tropical dry forests in Costa Rica (Becknell & Powers, 2014; Buzzard *et al.*, 2015) but contrast with studies carried out in tropical dry forests in Mexico (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013), suggesting geographical variation of trends in functional composition during succession amongst the spectrum of tropical dry forests.
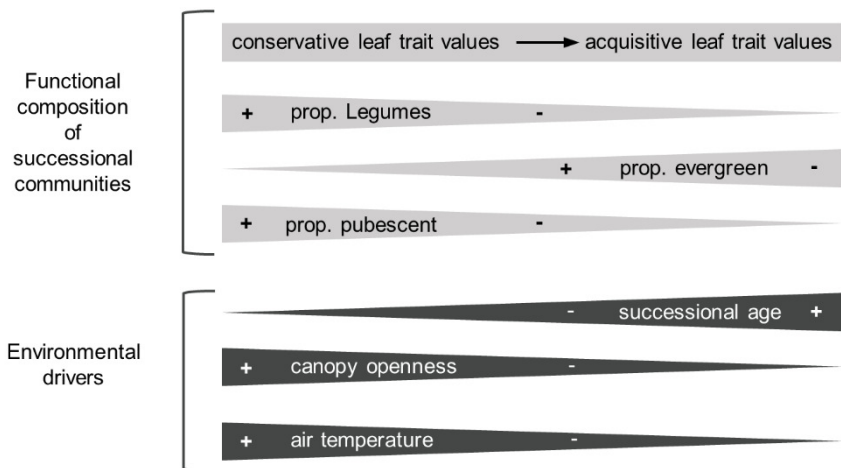
Figure 16. Overview of the changes in functional composition during secondary succession in tropical dry forest and their underlying environmental drivers. Prop. stands for proportion.

4.4.2 Importance of intraspecific variation of functional trait values

Partitioning of the variance of the whole dataset of leaf functional trait values across nested levels ranging from the leaf to the species showed that the variance of most traits was largely explained by between-species differences (on average 71.3% for non-chemical traits and 60.7% for chemical traits) (Figure 17). The amount of intraspecific variation was, however, not negligible. In paper IV, I consider this intraspecific variation, focusing on its importance in explaining changes in functional composition of communities in response to successional gradients and on intraspecific changes with ontogeny.

Figure 17. Partitioning of the variance of traits across nested levels of organisation (performed on 2539 leaves, 852 individual saplings, 69 species). Thickness stands for leaf thickness, Petiole for petiole length, LA for leaf area, SLA for specific leaf area, LDMC for leaf dry matter content,

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Density for leaf density, LPC for leaf phosphorous concentration, LCC for leaf carbon concentration, LNC for leaf nitrogen concentration, and C/N and N/P are leaf stoichiometric ratios.

Intraspecific variation along the successional gradient
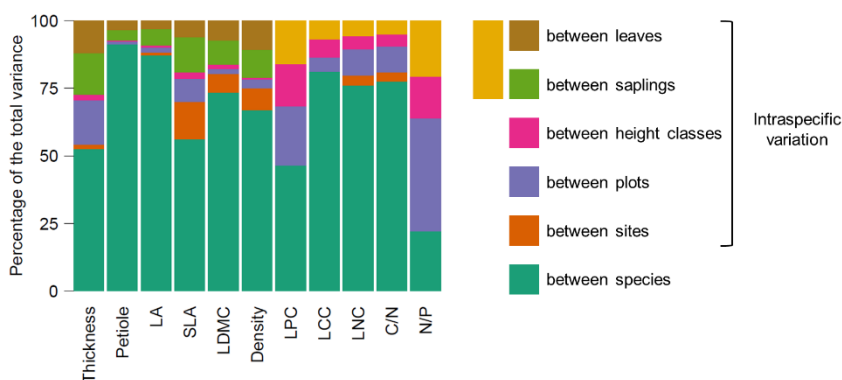
Both analytical approaches (multi- and single-trait) showed that the contribution of species turnover was more important than intraspecific variation in explaining the changes in community trait values during succession. However, the changes in community trait values that occur through intraspecific variation were strongly associated with the changes in environmental conditions during succession. This confirms the directionality of changes in trait values within species along environmental gradients found in other contexts (Lepš *et al.*, 2011; Bhaskar *et al.*, 2014; Carlucci *et al.*, 2015) and suggests a plastic response of trait values to environment. The response of community trait value through intraspecific variation was particularly important for morphological and chemical traits associated with leaf economics.

Intraspecific changes due to ontogeny

Five of the 11 continuous traits studied showed a directional change with ontogenic stage (using the proxy of sapling height divided by maximum height of the species): increase of leaf thickness, density, LDMC and LCC and decrease of SLA. This suggests a change from acquisitive to conservative strategies with ontogeny. If this trend extends beyond the short ontogenic window considered, as found by studies in other forest biomes (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014), this means that a tree growing in the successional forests studied would experience opposing changes due to succession (conservative to acquisitive) and ontogeny (acquisitive to conservative). Dynamic studies over larger ontogenic windows are needed to resolve the net outcome of these opposite changes.

4.5 The influence of changing abiotic and biotic environmental conditions during succession on the fate of seeds

This section presents and discusses preliminary results of the study of seed fate. I used GLMs to assess the influence of the site (intermediate-aged *versus* young secondary forest *versus* open area), litter treatment (with or without litter), predation treatment (with or without protection against predation) and species (seven) on two types of seed fate:

➢ seed removal, being the disappearance of a seed from the cluster, measured two weeks after the beginning of the experiment as a

proportion of the number of seeds initially placed in the cluster (after two weeks, the difficulty of relocating seeds made the assessment of this fate unreliable),

➢ seed germination, measured 12 weeks after the beginning of the experiment as the proportion of the number of seeds present at week two, which was the time of the first rain since the start of the experiment.

Characteristics of the seven studied species are presented in Appendix 1, characteristics of the three studied sites in Appendix 2 and the effect of the litter treatment and of the site on microclimatic conditions in Appendix 3.

4.5.1 Influence on seed removal

Model selection using the Akaike information criterion (AIC) resulted in a model with the site, the litter treatment, the predation treatment, the species and the interactions site * predation treatment, site * species, litter treatment * species and predation treatment * species (Table 2).

The presence of litter resulted in a large and significant decrease in seed removal, across species and for five of the seven species. This result is in line with the results of Cintra (1997) and suggests that leaf litter protects seeds by reducing the probability that they will be located by seed predators. Interestingly, the presence of litter was much more important in reducing seed removal than the treatment of protection from predation with a wire mesh, which was only significant in young forest and for the big-seeded species *Hymenaea courbaril*. The mesh of the wire used for this treatment (1.27 cm) excluded most vertebrates but not most insects that can remove small seeds (such as seeds of *Cochlospermum vitifolium* and *Stemmadenia obovata*, personal observation).

Seed removal was significantly higher in the intermediate-aged than in the young secondary forest and the open area when considered across species and for three species (*Astronium graveolens*, *Dalbergia retusa* and *Simarouba amara*) individually. This result is consistent with those of Wassie *et al.* (2010) and Souza-Silva *et al.* (2015), who found more predation under closed canopies, and suggests that there is a higher abundance of seed predators in intermediate-aged forests. Birds and rodents have been shown to frequent open sites less often (Da Silva *et al.*, 1996; Vieira & Scariot, 2006a). Consistently with the results of Vieira and Scariot (2006a), the effect of the site was dependent on the species: for *Hymenaea courbaril*, which is mainly predated by rodents (Asquith *et al.*, 1999), seed removal is significantly lower in the younger forest whereas for *Stemmadenia obovata*, mainly dispersed by birds, removal was significantly higher in the younger forest.

Although the responses to site and to litter and predation treatments was species-dependent, they do not seem to be related to seed size, presence of a hard coat, dispersal syndrome or successional status (Appendix 1). These traits are therefore inadequate proxies to enable understanding of the importance and type of predation and secondary dispersal, at least for the limited number of species that I studied.

Because I did not study the fate of the seeds after removal from the cluster, I cannot consider that the removed seeds have necessarily been predated. For some of the tested species, such as *Hymenaea courbaril*, scatter hoarding and seed burial by predators is known to be important and can lead to seed germination after secondary dispersal (Asquith *et al.*, 1999; Cole, 2009).

Table 2. Result of the selected GLM testing the response of the proportion of seeds that were removed to the experimental treatments. The values presented are the difference between the proportion estimated by the model for two categories of each treatment. Since all the explanatory variables are categorical, the values presented indicate the importance of the treatment effect. Significance tests are performed on the linear-predictor scale. Effects with a p-value < 0.001 are shown as ***, $p < 0.01$ as **, $p \leq 0.05$ as * and $p > 0.05$ as ns (non-significant). Significant effects are shown in bold. Species names are given in full in section 3.2.3, inter. stands for intermediate-aged secondary forest.

Treatment	Relative effect across species	per species						
		Astronium	*Cochlospermum*	*Dalbergia*	*Hymenaea*	*Simarouba*	*Stemmadenia*	*Thouinidium*
Litter treatment (with litter - without litter)								
overall	**-0.161** ***							
per species		-0.020 ns	**-0.373** ***	**-0.550** ***	**-0.103** **	-0.022 ns	**-0.164** *	**-0.088** *
Predation treatment (with protection - without)								
overall	-0.026 ns							
per site								
inter.	-0.092 ns							
young	**-0.037** *							
open	0.026 ns							
per species		-0.011 ns	-0.046 ns	0.079 ns	**-0.113** **	-0.038 ns	0.011 ns	-0.010 ns
Site								
overall								
inter - young	**0.194** ***							
inter - open	**0.176** ***							
young - open	-0.019 ns							
per species								
inter - young		**0.215** *	-0.039 ns	**0.691** ***	**0.190** *	**0.283** **	**-0.409** ***	0.093 ns
inter - open		**0.260** **	-0.100 ns	**0.672** ***	-0.043 ns	**0.276** **	0.060 ns	0.088 ns
young - open		0.045 ns	-0.061 ns	-0.019 ns	**-0.233** *	-0.007 ns	**0.469** ***	-0.005 ns

4.5.2 Influence on seed germination

Model selection for seed germination retained site, litter treatment, predation treatment, species and the interactions site * litter treatment, litter * predation treatment and litter treatment * species (Table 3).

Site (two ages of secondary forest or open area) was the treatment with the largest significant effect on seed germination. There was a higher germination rate in the two forests sites compared with the open site, consistent with previous results in tropical dry forests (Hardwick *et al.*, 1997; Alvarez-Aquino *et al.*, 2014). This can be explained by the canopy shade reducing air and soil temperature and increasing air humidity (Appendices 2 and 3), as suggested by studies using artificial shading and watering (Hardwick *et al.*, 1997; McLaren & McDonald, 2003a). Moreover, this amelioration of microclimate can reduce seed mortality by desiccation (Vieira & Scariot, 2006a).

The presence of litter had significantly positive overall effect on seed germination. This can be explained by the significantly higher air humidity and lower soil temperature under the litter (Appendix 3). However, the effect of the presence of litter was dependent on the site: it was only significant in the younger forest. In the open site, the litter was very thin and composed only of dry thatch remnants of the previous year's herbaceous vegetation. Its low effect on microclimatic conditions is probably not important enough to mitigate the hot and dry conditions of this site (Appendices 2 and 3). On the contrary, in the intermediate-aged forest, the relatively high humidity and low temperature provided by the canopy can be favourable enough for germination so that litter does not have an additional effect. The effect of the presence of litter was also species-dependent: it was only significantly positive for *Dalbergia retusa*, *Simarouba amara* and *Thouinidium decandrum*. As for seed removal, the analysed seed traits, dispersal syndrome and successional status did not explain the species-specific response to litter treatment.

The protection against seed predation had a positive effect on seed germination, both overall and through its interaction with the litter treatment. This effect is likely to be due to the fact that the reduced seed removal leaves more seeds able to germinate. In the same way, part of the observed effect of the presence of litter on the germination rate may be due to an indirect effect on seed removal.

Treatment	Relative effect	
Litter treatment (with litter - without litter)		
overall	**0.064**	*
per site		
intermediate forest	0.019	ns
young forest	**0.151**	***
open site	0.028	ns
per predation treatment		
with protection	0.023	ns
without protection	**0.088**	**
per species		
Astronium graveolens	- 0.064	ns
Cochlospermum vitifolium	0.006	ns
Dalbergia retusa	**0.187**	**
Hymenaea courbaril	-0.008	ns
Simarouba amara	**0.180**	**
Stemmadenia obovata	0.011	ns
Thouinidium decandrum	**0.257**	***
Site		
overall: intermediate - young forest	0.020	ns
overall: intermediate forest - open site	**0.204**	***
overall: young forest - open site	**0.184**	***
Predation treatment (with protection - without)		
overall	**0.103**	***

Table 3. *Result of the selected GLM testing the response of the proportion of seeds that germinated to the experimental treatments. The values presented are the difference between the proportion estimated by the model for two categories of each treatment. Since all the treatment variables are categorical, the values presented indicate the importance of the treatment effect. Significance tests are performed on the linear-predictor scale. Levels of significance are indicated as in Table 2.*

5   General discussion

5.1   Predictability of successional trajectories

I found that successional trajectories in tropical dry forests are quite unpredictable when taxonomic composition is considered. In paper II, I showed that the convergence of species composition of successional tropical dry forests towards the composition of old-growth forests is slow and the similarity of composition between successional and old-growth forests remains low even after several decades of succession. In paper III, I showed that the species composition of the assemblages of woody species regenerating under the canopy of isolated trees in pasture was poorly explained by the attributes of these trees. On the contrary, attributes of isolated trees explained relatively well the functional composition of the regeneration assemblage. Paper IV showed the directional changes in functional trait values of sapling communities during succession. These results support the hypothesis of a higher predictability of successional trajectories when considered in term of functional traits than taxonomic composition. Previous studies also found evidence supporting this hypothesis: for example, Dent *et al.* (2013) showed that successional tree communities in tropical moist forests increased in similarity with old-growth forests when considering species' shade tolerance but not species composition. Fukami *et al.* (2005) found a divergence in species composition but a convergence of functional group composition over time in experimental grassland.

This higher predictability of functional than taxonomic composition during tropical dry forest succession can be explained by the overlap of niches and of functional trait distributions of species (Violle *et al.*, 2012). Indeed, even if it is well established that species differ in their environmental requirements (contrary to the hypothesis of functional equivalence proposed by the neutral theory of Hubbell, 2005), species niches are not totally disjunct and a high number of species can establish and thrive in the same environment. This is the

idea of functional redundancy of species that, although mainly developed for the effect of species on their environment and the consequences for ecosystem functioning and conservation (Walker, 1992; Diaz & Cabido, 2001), can also be viewed in term of species response to their environment (Diaz & Cabido, 2001). While the functional traits of plants in a community are filtered by the abiotic and biotic environment, the identity of the species that successfully establish in successional forests is locally dependent on their presence in the surrounding landscape and their ability to be dispersed, and on stochastic events affecting their dispersal and establishment.

The higher predictability of changes in functional than taxonomic composition highlights the interest of considering community assembly through the lens of functional composition to get a better understanding of its drivers. When doing so, it is important to go back to the definition of functional trait, *i.e.* a "feature measurable at the level of the *individual*" (Violle *et al.*, 2007), and to take into account the variation of functional trait values within species, as an increasing number of ecologists advocate (Lepš *et al.*, 2011; Violle *et al.*, 2012; Laughlin & Messier, 2015)[9]. Increasing evidence for the importance of intraspecific variation of functional trait values compared with their interspecific variation shows the limit of an approach based on mean trait value per species (Hulshof & Swenson, 2010; Messier *et al.*, 2010; Siefert *et al.*, 2015). Mean values cannot take into account the plasticity of trait values within species in response to environmental conditions and therefore cannot inform on the importance of niche-overlap among species (Laughlin & Messier). Several studies have shown the importance of intraspecific variation of trait values in the response of communities to environmental gradients (Lepš *et al.*, 2011; Carlucci *et al.*, 2015), but the study presented in paper IV is the first, to the best of my knowledge, to do so for a successional gradient. It showed that, for some traits, the association between community trait values and environment was stronger (or even only detected) when considering intraspecific variation.

The study presented in paper IV showed that, besides their changes with environment, trait values also vary within species with ontogeny, as evidenced by previous studies (Thomas & Winner, 2002; Niklas & Cobb, 2008; Spasojevic *et al.*, 2014). To embrace the full range of trait values within species, appropriate sampling protocols are required (Violle *et al.*, 2012). Exhaustive sampling strategies such as the one I carried out for paper IV are time-consuming and therefore expensive (Baraloto *et al.*, 2010a). This generally result in a trade-off between the number of individuals per site and

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9. See also the post of Brian McGill on the blog *Dynamic ecology* (https://dynamicecology.wordpress.com/2015/07/01/steering-the-trait-bandwagon/)

species and the size and number of plots that can be studied. Sampling strategies therefore need to be carefully fitted to the processes and mechanisms targeted by the study and to the variability of the traits considered.

5.2 Difference in successional trajectories between tropical dry forests

Several of my results show or suggest that successional trajectories are not similar in all tropical dry forests. Here I discuss these results within the framework of the conceptual model presented in the introduction (Figure 1) and consider the influence of regional abiotic factors, landscape factors, past and present land uses and remnant vegetation on successional trajectories in tropical dry forests.

Tropical dry forests are encountered within a wide range of climatic conditions (see definition of tropical dry forests in section 1.5.1). This gradient, and especially climatic factors directly related to water availability, is expected to explain part of the heterogeneity of successional trajectories in tropical dry forests. Several of my results support this hypothesis. Paper I shows that the importance of positive and negative effects of established trees on the survival of seedlings beneath their crowns depends on the mean annual rainfall. The changes in plant strategies with succession observed for the tropical dry forests of Costa Rica (paper IV; Becknell and Powers, 2014; Buzzard *et al.*, 2015) differ from those observed in tropical dry forests of Mexico (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013). These two areas are at the opposite ends of the tropical dry forest climate gradient, with mean annual rainfall of ~ 1700 mm in Costa Rica and 900 mm in the Mexican site. This suggests that the trends of change in functional strategies during succession can vary along a gradient of precipitation within the range of tropical dry forests, although studies in other sites are needed to substantiate this hypothesis. The results of paper II, on the contrary, do not show support for the influence of the climatic gradient on successional trajectories, as indicated by species diversity and composition, even when assessing water availability, which is a more integrative index of climate than precipitation. Species diversity and composition are indices that ultimately result from several interacting mechanisms. Studying the changes in mechanisms and processes other than the ones tested in papers II and IV, by Becknell *et al.* (2012) (change in aboveground biomass) and by McDonald *et al.* (2010) (relative importance of seed *versus* vegetative reproduction) would allow the climatic categorisation of tropical dry forests to be refined. Interestingly, paper I and McDonald *et al.* (2010) both identified a possible switching point around 1400 mm of mean

annual rainfall and Becknell *et al.* (2012) found that tropical dry forests with more than 1500 mm had a greater rate of biomass accumulation during succession compared with drier forests. Conversely, considering the gradient of climatic conditions from dry to wet tropical forests could be a good alternative for functional ecology to their categorical classification.

The influence of landscape factors, past and present land uses and remnant vegetation on successional trajectories needs to be studied further. Paper II did not find any influence of previous land use on the rates of change in species richness or composition during succession. Paper III found that the effects of landscape factors were complex and site-dependent. Landscape and land-use factors are difficult to measure and the complexity of their effects cannot easily be synthesised in simple quantitative or qualitative indices. For example, the reporting of past-land uses by the studies reviewed in paper II did not give any quantitative and standardised information on the use of fire or the intensity of the past land use (*e.g.* in terms of intensity of grazing or number of cultivation cycles). Paper III shows that not only the presence but also the attributes of isolated trees in pasture influence the regeneration of woody species. Scaling up the results of individuals studies to wider spatial or temporal scales is therefore problematic. Despite these methodological challenges, the inclusion of more detailed landscape and land use factors in analysis of succession would improve understanding of their influence on successional trajectories (Chazdon, 2003; Chazdon *et al.*, 2007).

5.3   Implication for ecological restoration of tropical dry forests

When planning an ecological restoration project, the first step is to identify the objectives of the restoration and the opportunities and constraints of the site to be restored (Griscom & Ashton, 2011; Holl & Aide, 2011). In many cases, passive restoration, based only on natural regeneration, can be a valuable and relatively low-cost option when the objective is to recover a functional ecosystem with a high level of biodiversity. Paper II showed that secondary tropical dry forests have good resilience of their shrub and tree species richness and can reach levels of richness similar to those of old-growth forests in a few decades. Other studies have shown that this is also the case for aboveground biomass (Becknell *et al.*, 2012; Poorter *et al.*, 2016). In paper III, I found 126 species of trees, shrubs and lianas regenerating in three active pasture sites, which would be a promising starting point once the farming activity is abandoned. More generally, the *Área de Conservación de Guanacaste* where I carried out my fieldwork is a very good example of a successful restoration

programme mainly based on passive restoration (Janzen, 2002; Aronson *et al.*, 2005).

With respect to the opportunities and constraints of an area to be restored, it is important to assess the composition and abundance of the vegetation within and in the surroundings of the site. Paper III confirmed the importance of the presence of isolated trees within the site to facilitate regeneration (Guevara *et al.*, 1986; Schlawin & Zahawi, 2008; Griscom & Ashton, 2011). It also showed the importance of vegetation patches in the surroundings as seed sources and suggested the importance of scattered trees, living-fences and riparian vegetation to maintain connectivity within the landscape by acting as stepping stones and corridors for animal dispersers (Chazdon, 2014). Fire, grazing or the presence of vegetation limiting succession (such as invasive grasses planted in tropical pastures, Griscom & Ashton, 2011) are potential barriers to restoration. I have not studied these constraints in detail but I discuss them in paper II. When these constraints are present, intervention may be needed to remove them, as it is the case in the *Área de Conservación de Guanacaste* (Janzen, 2002).

With passive restoration, however, there is important uncertainty about the species composition of successional forests and their capacity to recover the full woody plant species composition of old-growth forests (paper II). If the objective of restoration is to re-establish a particular set of species, active restoration techniques (through sowing or planting) may be needed. Such intervention can also accelerate the re-establishment of the forest (Griscom & Ashton, 2011). In tropical dry forests, tree cover (continuous or in isolated trees or patches) has an overall positive effect on regeneration by attracting seed dispersers and mitigating harsh climatic conditions, and therefore increasing the establishment and survival of young woody plants (papers I and III and seed study). Species used for active restoration need to be carefully selected. Paper III showed that the attributes of the trees forming the first cover at the early stage of succession influence the composition of the assemblage of woody plants regenerating subsequently, hence suggesting a long-term legacy of the composition of the early stages. An approach based on functional traits can be valuable to guide the choice of species (Martínez-Garza *et al.*, 2005; Ostertag *et al.*, 2015). Paper IV suggests that species with conservative values of leaf traits can cope better with the open and hot environment of early succession, at least in the tropical dry forests of Costa Rica. Species with such leaf traits are therefore good candidates for active restoration. Legumes, which are abundant in tropical dry forests (Gentry, 1988), are also an interesting option: besides being able to thrive in the microclimatic conditions of the early stages of succession, many species are also able to fix nitrogen (Corby, 1988).

Selecting evergreen species has the advantage of providing shade even during the dry season and hence reducing the mortality risk for young woody plants establishing underneath (paper I). Paper III also showed that evergreen trees can foster the establishment of a larger number of species under their crowns. However, evergreen species are naturally less abundant in the early stages of succession and can be more sensitive to desiccating environmental conditions (paper IV).

Once the canopy cover is closed and the microclimate changes towards more shaded, cool and moist conditions, species with more acquisitive leaf trait values should start establishing. If this is not the case, it could be a sign of dispersal limitation for these species and enrichment planting might be needed.

6 Critical assessment and future research

6.1 Critical assessment of my PhD research

Two papers (I and II) are based on a systematic review of the scientific literature. The relatively low number of studies included in these reviews (29 studies in paper I and 13 datasets from 9 studies in paper II[10]) confirms that the tropical dry forest biome receives relatively less attention from scientists than other tropical forest biomes and that more studies are needed (Sanchez-Azofeifa *et al.*, 2005; Vieira & Scariot, 2006b; Quesada *et al.*, 2009). The qualitative and quantitative analyses conducted in papers I and II would need to be renewed once more studies become available. For paper I, the low number of studies was one factor preventing the use of a meta-analysis approach. The analysis conducted to test the stress gradient hypothesis is a vote-counting approach, an approach less powerful than a meta-analysis because it does not enable an overall effect-size to be calculated and the studies to be weighted by their precision (Koricheva & Gurevitch, 2014). Extending this analysis to the whole climatic range of tropical forests would likely have led to the inclusion of a larger number of studies enabling the use of a meta-analysis, but at the cost of reducing the paper's focus on tropical dry forests. For paper II, however, the number of studies included was sufficient to get very robust results (as shown by the fail-safe numbers). Papers I and II also showed an unbalanced distribution of the research effort between tropical dry forest regions. Sixty-nine per-cent of the studies included in paper I and 92% of the datasets included in paper II were conducted in the Neotropics, whereas

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[10] The inclusion of a study in the meta-analysis conducted in paper II was dependent on the availability of raw data. The number of studies that could potentially have been included, but for which I did not manage to contact the authors or I did not get the agreement to use the data, was roughly ten.

Miles *et al.* (2006)[11] estimate that 67% of tropical dry forests are located in this region. This is consistent with research showing an overall unbalanced distribution of ecological studies in the tropics (Stocks *et al.*, 2008; Powers *et al.*, 2011). The results of these two papers, and especially paper II, should be considered with caution for African and Asian dry forests where the size of the species pool, floristic composition, disturbance history and forest fauna differ (Corlett & Primack, 2006; Dexter *et al.*, 2015; Slik *et al.*, 2015).

Two main observational approaches are used to study succession in forests: the dynamic approach monitoring the changes occurring in permanent plots over time, and the chronosequence based on a space-for-time substitution (Chazdon, 2014). The long temporal scale of succession in forests makes the former approach more difficult and hence less commonly used in tropical forests (Chazdon *et al.*, 2007; Chazdon, 2014). Several studies in this thesis are based on a chronosequence approach (papers II and IV, and the study of seed fate). This approach has potential biases. The environmental conditions of the study sites at the beginning of secondary succession and history of land use are usually difficult to know with accuracy, which results in a risk of wrongly attributing to an effect of succession differences that are simply due to variation amongst sites (Pickett, 1989; Chazdon, 2014). Moreover, there is possible confounding between site conditions and time of abandonment (Chazdon, 2003): for example, agricultural activities are likely to be abandoned in less fertile sites earlier than in more fertile ones. Several studies have used a combination of chronosequence and dynamic approaches (over less than 10 years) to test if the predictions resulting from analysis of chronosequences match those of the dynamic approach. Maza-Villalobos *et al.* (2011a) found that neither the trends observed for forest structure, nor for species diversity, with the chronosequence approach were consistent with those of the dynamic approach. Chazdon *et al.* (2007) showed that predictions related to forest structure were better than those of species diversity, while Mora *et al.* (2015) showed the opposite, and Lebrija-Trejos *et al.* (2010a) found that both were well predicted. To the best of my knowledge, no such studies have been conducted to test the validity of the chronosequence approach for changes in functional diversity or composition. Because of the higher predictability of changes in functional than taxonomic composition (see section 5.1), the chronosequence approach can be expected to perform better for changes in functional composition. Despite its limitations, the chronosequence approach is recognized as a useful and pragmatic approach for assessing long-term trajectories of succession (Quesada *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a), as it is the case in paper II.

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[11] See section 1.5.1 for details on the methods used in this study.

A strength of my field-based studies and a way to mitigate part of the limitation of the chronosequence approach is the measurement of environmental factors in successional plots. For paper IV and the study of seed fate, I measured microclimatic conditions in each successional plot (see section 3.2.4 for details). The changes in microclimatic conditions are often assumed but rarely measured in successional studies (but see Lebrija-Trejos *et al.*, 2011). Measuring these factors allows a more direct test of their effects on the observed changes in plant communities with site successional age. For paper IV, I also included measurements of soil physical and chemical factors. These factors were generally not significantly correlated with successional age, which shows that there is limited risk of confounding between environmental conditions and successional age. For paper III, measuring microclimatic conditions under isolated trees would have enabled the effects of isolated tree attributes on regeneration through amelioration of environmental conditions to be tested more directly. However, because of the need to take repeated measurements at different times of the day and year to correctly assess microclimatic factors, this approach was impractical given the large number of isolated trees studied.

Soil factors, frequency and intensity of fire events, grazing and competition with exotic grasses are important factors affecting secondary succession (as reviewed in section 1.2.2) but are not a major focus of my study. Soil factors are considered in paper IV through the separation of the two forest types (which differed in soil factors) in the statistical analyses and the results showed the differences in their effects on community functional trait values of the sapling communities. In the study sites of paper IV and the study of seed fate, and more generally in the *Área de Conservación de Guanacaste*, efficient control of fire and exclusion of grazing are implemented as a way of allowing natural succession (Janzen, 2002) and are therefore not a major constraint, at least within the limits of the protected area. The differences observed in regeneration assemblages among the three pasture sites studied in paper III are likely to result partly from differences in grazing intensity, fire history and intensity of the competition with established grass vegetation. However, the high number of individuals and species surveyed (including a high proportion with a height exceeding that of the grass cover) suggests that the effect of these factors is not strong enough to inhibit woody plant regeneration.

The functional traits measured in paper IV are commonly used in ecological studies and their association with resource economics and tolerance of dry and hot conditions is well established (Wright *et al.*, 2004; Poorter & Markesteijn, 2008; Reich, 2014). However, they are all leaf morphological, chemical or phenological traits which are only indirectly related to the function of interest

(they are sometimes qualified as "soft traits", Violle *et al.*, 2012). The measurement of physiological traits directly associated with the functions of interest for the study ("hard traits"), such as photosynthetic capacity and leaf dark respiration rate for resources economics, and C-isotope composition and leaf water potential for drought tolerance (Wright *et al.*, 2004; Markesteijn *et al.*, 2011; Perez-Harguindeguy *et al.*, 2013), would have been valuable. I did consider measuring some of these traits. However, besides the logistical difficulties of accessing equipment and consumables in the field, the time required to measure these traits reliably was not compatible with the extensive sampling design of this study. For leaf phenological traits (included in papers III and IV), I used a coarse categorisation of leaf phenological habit based on expert knowledge. However, species range along a continuum of phenological behaviour (Borchert, 1994) and categorisation is a simplification. Accurately assessing leaf phenological behaviour requires regular (at least-monthly) monitoring of several individuals per species over several years, which was incompatible with the time frame of my PhD research. Such information is available for a number of species in my study area (Borchert, 1994), but not for enough of them to be useful for community studies.

The hypothesis of phylogenetic conservatism predicts that species conserve the ecological characteristics of their ancestors (Ackerly, 1999; Mouquet *et al.*, 2012). Evolutionary close species are therefore expected to have closer values of traits than expected by chance (the phylogenetic signal). As a consequence, species should not be considered as independent for analysis of trait associations, and statistical methods taking into account the phylogenetic signal should be used, such as the phylogenetically independent contrast method (PIC, Felsenstein, 1985). However, I did not use such a method when looking at traits associations to assess plant strategies (appendix D in paper IV), which leads to a risk of confounding bias by evolutionary relationships between species. However, for 87 species of the same study area, Powers and Tiffin (2010) did not find any strong phylogenetic signal in functional trait data, once species of the Leguminosae family were excluded. Similarly, Pringle *et al.* (2011) did not find a phylogenetic signal in 30 species of Mexican tropical dry forests. At the community scale, most studies do not support the hypothesis of a correlation between functional and phylogenetic diversity (Garnier *et al.*, 2016), suggesting a decoupling of functional and phylogenetic structures of communities.

Lastly, time constraints have imposed some trade-off in methodological choices. For example, I would have liked to be able to include more plots for paper IV to improve statistical power, but the necessity to sample a large number of individuals per species and per plot to assess the intraspecific

variation prevented that. For the experimental study of seed fate, using a larger number of species may have enabled trends associated with seed traits to be detected.

6.2 My short-term research priorities

Building on the results of my doctoral work, there are several research ideas that I would like to develop. In the immediate future, I plan to work on two studies for which I have already collected data during my PhD:

➢ To study the influence of established trees and of changing environmental conditions during succession on the growth and survival of seedlings, I have set up an experiment similar to the study of seed fate. I planted seedlings of six species in the two successional forests and applied two treatments (presence or absence of litter and exclusion of root interactions through trenching). I monitored the survival and growth of these seedlings from 2013 to 2015. I measured microclimatic factors in every plot. In 2015, I measured a set of traits (leaf, stem and root) on several individuals per species and per plot. I plan to analyse these data with four main objectives: (1) identify the mechanisms through which established trees influence regeneration, (2) identify the establishment strategies of the studied species (in terms of the potential trade-off between growth and survival), (3) understand the link between functional traits and establishment strategies, considering variation between and within species, and (4) test for a possible effect of abiotic and biotic environmental conditions on intraspecific variation in functional trait values.

➢ For paper IV, I worked in permanent plots of the research group of Dr Jennifer Powers (University of Minnesota). For these twelve plots and six additional ones, Jennifer Powers' team have surveyed all adult trees and have data on the seed rain and soil seed bank. I also surveyed the saplings and seedlings. We now intend to analyse these data together to study the changes in species and functional composition (using basic traits such as dispersal syndrome and leaf phenological habit) across successional and life stage gradients with the objective of assessing the directionality of these changes and identifying the life stages (from seed dispersal to adult stages) that are the most critical for tree establishment.

In a relatively longer term, there are several ideas I would like to explore:

➢ Building on paper IV, I would like to further study the intraspecific variation of functional traits with ontogeny and environmental

conditions and the importance of intraspecific variation for fitness of plant species and community assembly processes along environmental gradients.

➢ I would also like to go beyond the leaf economics spectrum and contribute to the timely question of the existence of a spectrum of strategies at the scale of whole plants (Baraloto *et al.*, 2010b; Reich, 2014). I would be interested to study the patterns of correlation of leaf, stem and root traits to understand the response of individual plants and tree communities to changes in their environment and the resulting effects on ecosystem processes.

➢ Expanding on papers II and IV and the work of Lohbeck and colleagues (Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015), I would like to use a meta-analysis approach to study if the directionality of change in resource acquisition strategies (considering the more commonly studied traits such as SLA and leaf phenological habit) during succession varies along the precipitation gradient in tropical forests. I would test the hypothesis that at the extreme dry end of the gradient of precipitation, the main axis of change is related to drought-coping strategies (Lebrija-Trejos *et al.*, 2010b; Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015), then moves to a change from conservative to acquisitive strategies at the upper end of the range of tropical dry forests (Becknell and Powers, 2014; Buzzard *et al.*, 2015 and paper IV) and finally switches to a change from acquisitive to conservative strategies in tropical wet forests (Lohbeck *et al.*, 2013; Lohbeck *et al.*, 2015).

6.3   Recommendations for future research

Besides the research plans mentioned in the previous subsection, my PhD research supports the need for further studies on several topics.

There is a general need to increase research on the ecology of tropical dry forests to better understand how they differ from other tropical forest biomes (Sanchez-Azofeifa *et al.*, 2005; Quesada *et al.*, 2009). A focus on less studied regions (Africa, Asia and the Pacific area) is especially important. Moreover, standardised protocols and multi-site research projects (Quesada *et al.*, 2009) would be especially valuable in enabling the effect of regional-scale factors (such as climate, and the plant and animal species pool) to be tested.

As mentioned in section 5.2, several factors likely to affect successional trajectories need to be tested further: landscape factors, past and present land uses and remnant vegetation. Multi-disciplinary approaches using field-based ecological studies, remote sensing and social science would be particularly

interesting (Sanchez-Azofeifa *et al.*, 2005; Castillo-Nunez *et al.*, 2011; Chazdon, 2014).

More studies assessing the relative contributions of deterministic and stochastic components in succession, such as the study of Norden *et al.* (2015) showing their equal contribution to successional dynamics in neotropical forests, are needed to inform theoretical models of succession. Vellend *et al.* (2014) critically reviewed appropriate methods to do so, such as the use of null models in observational studies or experimental approaches manipulating the order of colonisation of different species during succession, though the latter approach would be difficult for long-lived organisms such as trees.

The importance of intraspecific trait variation is increasingly acknowledged. As mentioned in the previous section, it is now important to assess the processes (environmental drivers and ontogeny) driving this variation (Lepš *et al.*, 2011; Violle *et al.*, 2012; Spasojevic *et al.*, 2014), as well as the spatial scales at which they affect community assembly (Siefert *et al.*, 2015; Spasojevic *et al.*, 2016). Such studies will help to refine sampling protocols to study the changes in community-level trait values with environmental gradients. Lastly, distinguishing the contributions of genetic variation and phenotypic plasticity to intraspecific variation in functional trait values is important, not only for ecological theory but also for application to ecological restoration. A strong contribution of genetic variation would emphasise the importance of considering the provenance of propagules used for direct seeding or planting. On the other hand, if phenotypic plasticity is the main mechanism causing intraspecific variation, using species with a high plasticity could be valuable to mitigate unexpected changes in environmental conditions that could result from local disturbance or global climate change. To assess the relative importance of genetic variation and phenotypic plasticity, experimental studies are needed, including the use of long-established methods such as common garden and transplant experiments.

7 Conclusion

Tropical dry forests are fascinating environments, especially for the variety of their colours and ambiance changing with the seasons. They are also endangered ecosystems that have been threatened by human activities for a very long time. The increasing attention that they are receiving from scientists, managers and the general public is a positive sign for their future.

In the last two or three decades, studies of the ecology of tropical dry forests have led to the recognition of their specific characteristics and the need to move beyond the extrapolation to these forests of ecological models that have been developed in tropical moist and temperate forests. They have also shown heterogeneity among tropical dry forests. Successional trajectories, because of the complexity of the multiple interacting factors influencing them, still appear to be very context-dependent. Further research is therefore needed to identify the relative importance of these factors, especially regarding the role of the landscape and the legacies of past land uses, and to get a more unified understanding of the driving forces of succession across tropical dry forests.

Awareness-raising and involvement of the general public, and especially of the population living in surrounding areas, is of the utmost importance for the conservation and restoration of tropical dry forests. Initiatives such as the educational and ecotourism programs led by the *Área de Conservación de Guanacaste* are playing a great role in demonstrating the richness and fragility of these forests and encouraging the local population and visitors to contribute to their protection and restoration.

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Appendices

Appendix 1. Characteristics of the species tested in the study of seed fate.

Species	Family	Seed mass (g)[1]	Seed size (mm³)[1]	Presence of hard seed coat[1]	Dispersal mode[2]	Successional status[3]
Astronium graveolens	Anacardiaceae	0.013	13.6	no	anemochorous	late succession
Cochlospermum vitifolium	Bixaceae	0.023	25.4	yes	anemochorous	early succession
Dalbergia retusa	Leguminoseae	0.060	63.5	no	anemochorous	generalist
Hymenaea courbaril	Leguminoseae	3.205	2444.1	yes	zoochorous	mid to late succession
Simarouba amara	Simaroubaceae	0.855	1262.4	yes	zoochorous	mid to late succession
Stemmadenia obovata	Apocynaceae	0.060	69.7	no	zoochorous	mid to late succession
Thouinidium decandrum	Sapindaceae	0.062	181.6	no	anemochorous	generalist

1. Data from Géraldine Derroire (unpublished), average of the measurement of 25 seeds.
2. Data provided by Powers and Tiffin (2010) supplemented by information obtained from local experts (Roberto Espinoza and Daniel Perez Avilez).
3. Data provided by Leland Werden and Jennifer Powers (unpublished) based on the analysis of species abundance in a chronosequence of 84 plots in the *Área de Conservación de Guanacaste* and in Palo Verde (Costa Rica).

Appendix 2. Characteristics of the three sites used in the study of seed fate.

	Sites		
	Open site	Young secondary forest	Intermediate-aged secondary forest
Successional age (years)	0	~ 15	~ 30
Proportion deciduous (%)[1]	NA	72.7 [a]	56.7 [a]
Proportion zoochorous (%)[1]	NA	37.4 [a]	70.9 [a]
Canopy height (m)	NA	15.2 [a]	17.8 [a]
Canopy openness (%)			
dry season	100 [a]	22 [b]	12 [c]
wet season	100 [a]	10 [b]	8 [c]
Air temperature (°C)			
dry season	29.4 [a]	28.1 [b]	26.7 [c]
wet season	26.7 [a]	25.2 [b]	24.5 [c]
Red : Far red ratio	0.56 [a]	0.38 [b]	0.77 [a]

1. Proportion of the basal area of all trees with DBH $\geq$ 1 cm measured in a circular plot of 10 m radius centred on the seed plot.
All data from Géraldine Derroire (unpublished).
Letters indicate significantly different values (t-test, ANOVA or Kruskal-Wallis test and post-hoc test).

Appendix 3. Effect of litter treatment and site on microclimatic conditions in the study of seed fate.

	Effect of litter treatment	Effect of site[1]	Effect of interaction site * litter treatment
Soil temperature[2]	**p = 0.031**	**p < 0.001**	p = 0.898
	litter < no litter	inter. < young < open	
Soil moisture[2]	p = 0.459	p = 0.066	p = 0.331
Air humidity[2]	**p = 0.017**	**p < 0.001**	p = 0.846
	no litter < litter	open < young < inter.	
Litter depth	**p < 0.001**	**p < 0.001**	**p < 0.001**
	no litter < litter[3]	open[4] < young < inter.	

1. *Inter.* stands for intermediate-aged forest, *young* for young forest and *open* for open site.
2. Measured during the wet season.
3. This is a direct consequence of the litter removal.
4. In the open site, the litter is not woody plant leaf litter but rather dry material from the growth of herbaceous plants (thatch) in the previous year.
All data from Géraldine Derroire (unpublished).
p-values were obtained from two-way ANOVAs, results that are significant at p < 0.05 are shown in bold.