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View from the top of the Inselberg at sunrise
Nouragues Ecological Research Station, French Guiana

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GENERAL INTRODUCTION

I.   The uncertain future of tropical forests: crucial ecosystems under threat

The Earth's vegetation has long been perceived as a passive land component, at the mercy of spatial and temporal climate fluctuations. This historical view has been initiated by naturalist expeditions in the 18th century, which led to flora distribution maps and also laid the key concepts of biogeography (Humboldt 1849; Grisebach 1872). Köppen (1936), for instance, proposed an influential map of natural vegetation distribution, which mirrored local climatic conditions and is still currently used to define climate zone boundaries (Kottek *et al.* 2006). How climate influences individual plant functioning and species distribution has since become a central theme in plant ecophysiology (Holdridge 1947; Mooney, Pearcy & Ehleringer 1987).

Charney (1975) initiated a change of paradigm, suggesting vegetation has a critical influence on climate. He showed that the extremely sparse vegetation in the Sahara, and the consequent strong reflection of solar radiation, reinforce the aridity of the region through a positive feedback. The coupling of climate and vegetation dynamics is now widely recognized. Evidence encompasses all biome types and reveals a diversity of biophysical and biogeochemical feedback mechanisms, from the vegetation effect on the land surface albedo to the exchange of gases and aerosols (Pitman 2003; Moorcroft 2003; Meir, Cox & Grace 2006). In this coupled dynamics of the Earth system, tropical forests take on a major role.

1. Crucial role of tropical forests in the Earth system

Globally, forests represent about 30% of the Earth's land surface, store almost half of the terrestrial carbon (Fig. 1), contribute to about half of the global land gross primary productivity, and constitute a net carbon sink (Bonan 2008; Beer *et al.* 2010; Pan *et al.* 2011). Trees store approximately as much of the excess fossil carbon generated by our societies as

the atmosphere or the oceans[1]. Covering just 7% of the Earth's land surface, tropical forests play a disproportionate role: they store about 25% of terrestrial carbon and contribute to over a third of the global terrestrial productivity (Bonan 2008). They also recycle about a third of the precipitations through evapotranspiration and thus contribute to generate and maintain a humid climate regionally (Eltahir & Bras 1994; Boyce *et al.* 2010; Harper *et al.* 2013) with positive effects also extending well beyond the tropics (Lawrence & Vandecar 2015; Devaraju, Bala & Modak 2015). In particular, Amazonia[2] represents the largest continuous tropical forest in the world, covering about 5.4 millions km^2 (Malhi *et al.* 2008), and contributes to about half of the ca. 250 Pg of carbon hold in tropical forest (Feldpausch *et al.* 2011; Saatchi *et al.* 2011). This role of tropical forests on climate and atmospheric CO_2 levels put them at the forefront of policy-driven climate change mitigation effort (Agrawal, Nepstad & Chhatre 2011).
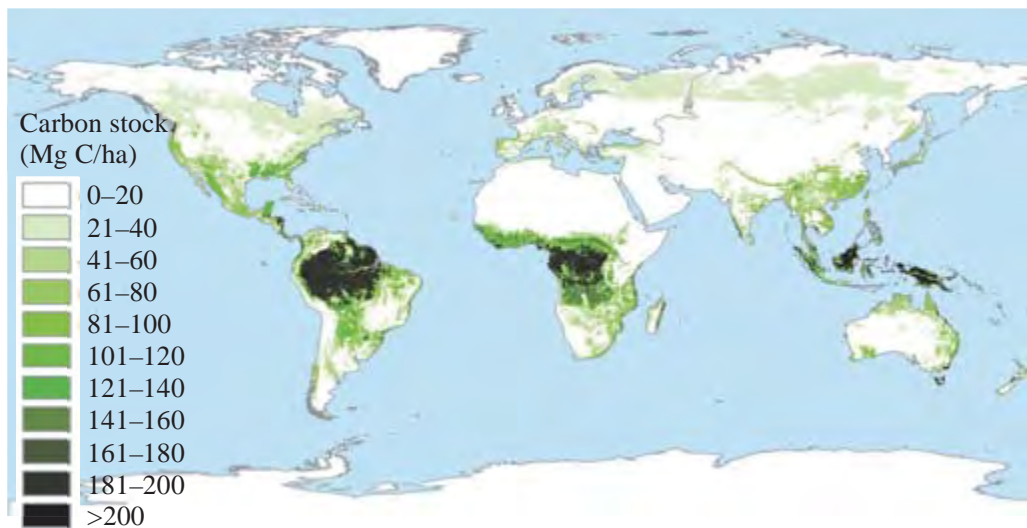
Fig. 1. Global total biomass carbon density, in MgC/ha. From Pan *et al.* 2013.

Tropical forests also host over half of the Earth's biodiversity (Scheffers *et al.* 2012). The myriad of shapes and functions these tropical ecosystems shelter has nurtured the development of biogeography and theories on diversity and evolution (Wright 2002), starting with the seminal expeditions of Alexander von Humboldt or Alfred Russel Wallace. This biological diversity provides important ecosystem services[3] to ca. 1.2 to 1.5 billion people

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[1] Global carbon project, http://www.globalcarbonproject.org/
[2] Considering this strong role of Amazonia and in consistency with the rest of this thesis, the present introduction focuses primarily on Amazonian forests, however recognizing that African, Indo-Malayan and Australasian tropical forests are also important.
[3] Ecosystem services are the benefits people obtain from ecosystems. These include (i) provisioning services

who directly rely on tropical forests for food, timber, or medicines (Byron & Arnold 1999; Vira, Wildburger & Mansourian 2015). Among this large global population, about 60 million indigenous people almost solely depend on forests. In particular forest wild fruits, nuts, vegetables, mushrooms and animal products contribute in many ways to food security and sustainable diets, hence to human health (Vinceti *et al.* 2013; Ickowitz *et al.* 2014; Dawson *et al.* 2014). Several major plant crops of critical importance globally, such as palm oil, coffee, or rubber, come from tropical forested areas (Fig. 2a). More generally, more than 650 tropical tree species have been mentioned as important to smallholders' livelihoods in agroforestry systems (Orwa *et al.* 2009). As an other illustrative example of these biodiversity benefits, more than 250 plants have been identified in the traditional materia medica of Amerindian communities in French Guiana (Grenand *et al.* 2004; Odonne *et al.* 2011; Fig. 2b). Also they use more than 50 plant species in their traditional basketry for tools for cooking, fishing or hunting as well as fineries (Davy 2007, 2010; Fig. 2c).
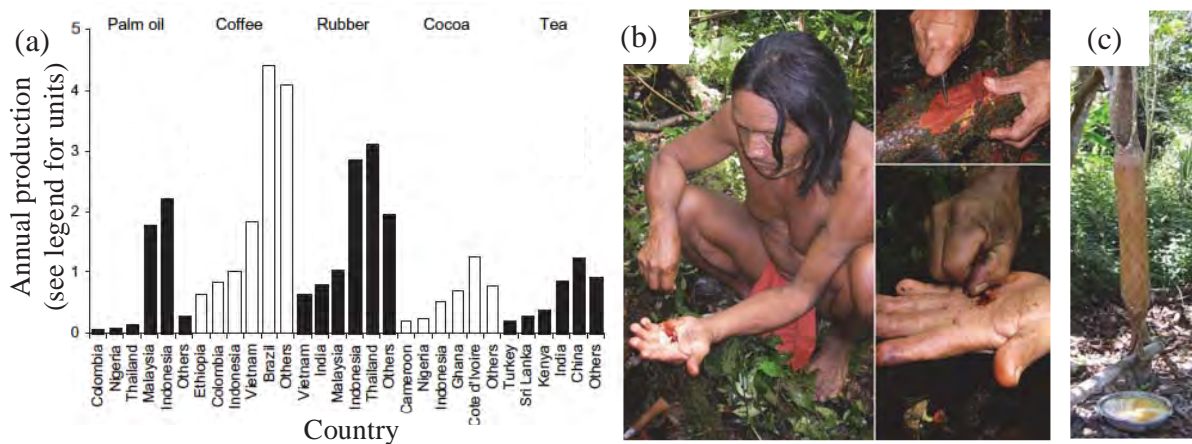
Fig. 2. Examples of global products and local traditional uses of tropical forest plants. (a) Average annual production for five tree commodity crops for key production countries. Units of production are: palm oil, 10s of millions of tons; coffee, 10s of millions of 60 kg bags; rubber, cocoa and tea, millions of tons. Figures are based on the following years: palm oil, coffee and cocoa, 2008/2009 to 2010/2011; rubber and tea, 2007 to 2009. From Dawson *et al.* 2014. (b) Preparation of a phytotherapeutic remedy for leishmaniasis by extraction of stem juice from *Callichlamys latifolia* by an Amerindian from the Oyapock basin in French Guiana. 38 different species have been reported to be used in medicinal recipes to treat leishmaniasis locally. From Odonne *et al.* 2011. (c) A traditional piece of basketwork involved in cassava preparation, Oyapock basin, French Guiana. From Davy 2007.

However, together with atmosphere, oceans and vegetation, another major player has come up over the Earth scene. As the world has entered the Anthropocene – a new geological

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such as food, water, timber, and fibre; (ii) regulating services that affect climate, floods, disease, wastes, and water quality; (iii) cultural services that provide recreational, aesthetic, and spiritual benefits; and (iv) supporting services such as soil formation, photosynthesis, and nutrient cycling (Millennium Ecosystem Assessment 2005; Vira, Wildburger & Mansourian 2015).

period, defined by humanity's massive impact on the planet (Crutzen 2002; Schimel, Asner & Moorcroft 2013; Lewis & Maslin 2015) -, critical ecosystem services are put at risk (Millennium Ecosystem Assessment 2005). Tropical forests are under strong human pressure through logging and forest-to-pasture conversion, and may durably face a warming and more variable climate due to anthropogenic greenhouse gases emissions (Malhi *et al.* 2008; Lewis, Edwards & Galbraith 2015), calling their future into question. Far from the fantastic and mysterious images of tropical "unexplored territories[4]", that were the sceneries of Edgar Rice Burroughs[5] or Rudyard Kipling[6]'s novels, it took less than a century to make tropical forests henceforth evoke true stories, in which Mowgli or Tarzan are not the only humans anymore.

2. Tropical forest vulnerability to perturbations

a. Historical changes in tropical forest cover

Different routes can be used to understand the extent to which tropical forests are vulnerable to perturbations. A first route is to analyse the paleo-record and forest response to past climatic events. These represent natural experiments at the scale of ecosystems.

In some areas, continuous palynological and fossil records have provided evidence of tropical forests dominance since the late Cretaceous or early Tertiary (Wing *et al.* 2009; Jaramillo *et al.* 2010; Morley 2011). However, tropical regions have experienced a range of climatic conditions through the Cenozoic, which have probably induced vegetation changes. For example, variation in Neotropical floral diversity have been shown to be coordinated to temperature fluctuations from the late Paleocene through the Eocene (Jaramillo, Rueda & Mora 2006). However, we are currently lacking the tools to document vegetation response to climatic change over this long time scale.

In Amazonia, climate changes and fires occurred through the Quaternary (Bush *et al.* 2002; Bush, Silman & Urrego 2004; Mayle *et al.* 2004; Power *et al.* 2008), with a documented decline in precipitation and a decrease in temperature during the Last Glacial Maximum. However there is no clear evidence of large changes of forest state during this

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[4] Literal translation of the Sanskrit word "jangala", from which the word "jungle" originates.
[5] *Tarzan of the Apes*, 1912
[6] *The Jungle Book*, 1894

period in latin America, which may have been restricted to ecotonal areas (Colinvaux, De Oliveira & Bush 2000; Bush *et al.* 2004; Mayle *et al.* 2004). This is in contrast with the situation of tropical Africa, which underwent clear changes in forest cover (Bonnefille & Riollet 1988; Maley 1991). The most significant changes in tropical forest cover may have occurred during the Holocene during which important dry events (Mayle *et al.* 2004; van Breukelen *et al.* 2008) probably favoured savannah and semi-deciduous forest over humid evergreen rainforests in some tropical areas (e.g. Mayle *et al.* 2007). Overall, direct paleo-ecological evidence, even though scattered in space and time, suggests that tropical forests have been resilient to past climatic fluctuations, which have resulted in smooth floristic assemblage shifts rather than in abrupt transitions (Chave 2014).

However, the current threats to tropical forests are of unprecedented pace. There is now an increasing consensus on a projected increase in seasonality in tropical regions, with more frequent and intense droughts (Touma *et al.* 2015; Duffy *et al.* 2015; Chadwick *et al.* 2016), simultaneous to a fast warming and increase in atmospheric CO_2 concentrations (IPCC 2013). These effects are added to direct anthropogenic pressures through deforestation and forest degradation (Hansen *et al.* 2013; Lewis *et al.* 2015). Thus future changes in tropical ecosystems may have no analogue to past changes (Cowling *et al.* 2004).

b. Current evidence for tropical forest vulnerability.

A much finer approach to study tropical forest vulnerability to perturbations relies on monitoring current forest dynamics. Permanent sample plots, where all trees above a certain minimum size are tagged, mapped, and with their diameter recorded repeatedly at regular intervals (Malhi *et al.* 2002; Anderson-Teixeira *et al.* 2015), have offered important insights in tropical forest dynamics over the past decades. Some studies have reported an increase in forest biomass stocks (Phillips *et al.* 1998; Baker *et al.* 2004; Chave *et al.* 2008; Lewis *et al.* 2009) and also tree growth rates (Lewis *et al.* 2004) over the past decades. But a recent analysis using a compelling distributed network of 321 plots across Amazonia revealed a long-term decreasing trend of this carbon accumulation, due to an increase in biomass mortality together with a growth rate increase levelling off (Brienen *et al.* 2015, Fig. 3).

However permanent plot studies remain mostly descriptive and are thus not well suited to explore and disentangle the different mechanisms underlying the trends they revealed. For example, the mechanisms explaining the observed increase in forest biomass have been largely debated. It could have resulted from climatic drivers. For example, the increase in CO_2

atmospheric concentration may increase leaf light-use and water-use efficiencies, and thus induce a so-called CO_2-fertilization effect. Also increased nitrogen deposition due to anthropogenic activities (Vitousek *et al.* 1997; Peñuelas *et al.* 2012) may have allowed increasing photosynthetic capacities and forest productivity (e.g. Tanner, Kapos & Franco 1992). Alternatively, the observed changes in forest structure may reveal forest slow recovery from past natural and human disturbances (Chazdon 2003). Indeed, indigenous populations in forests may have been larger than usually believed over the past centuries (e.g. Denevan 1992).
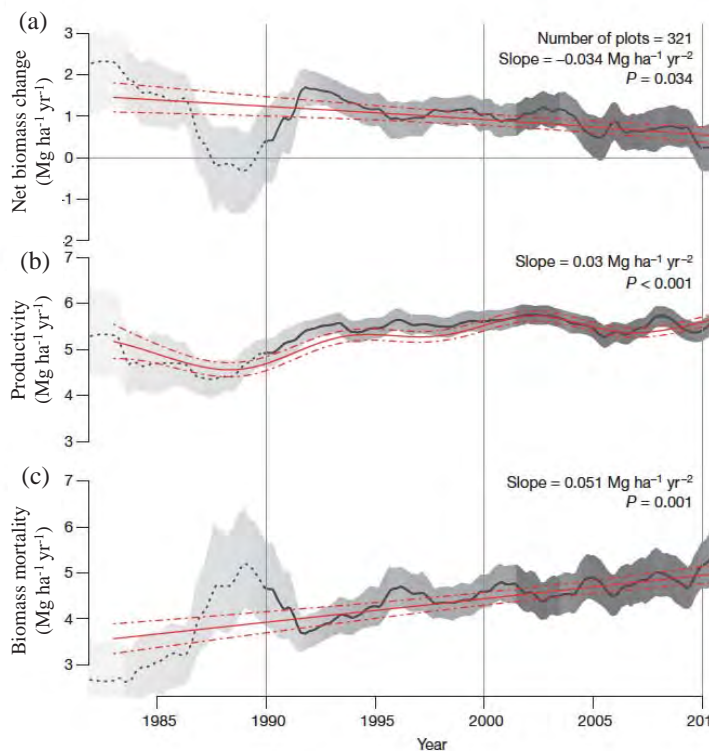
Fig. 3. Trends in (a) net above-ground biomass change, (b) productivity and (c) mortality across 321 sites in Amazonia, reported in Brienen *et al.* 2015. Black lines show the overall mean change up to 2011 for 321 plots weighted by plot size, and its bootstrapped confidence interval (shaded area). The red lines indicate the best model fit for the long-term trends since 1983 using general additive mixed models (GAMM), accounting explicitly for differences in dynamics between plots (red lines denote overall mean, broken lines denote s.e.m.). Estimated long-term (linear) mean slopes and significance levels are indicated. Shading corresponds to the number of plots that are included in the calculation of the mean, varying from 25 plots in 1983 (light grey) to a maximum of 204 plots in 2003 (dark grey). From Brienen *et al.* 2015.

When exploring community composition, permanent plot studies revealed non-random changes in floristic composition that may provide insights on the potential drivers of forest structural changes. Some studies found an increase in fast-growing species, most in agreement with a fertilization effect (Laurance *et al.* 2004; Körner 2004). Others did not (Chave *et al.* 2008) or conversely found an increase in dominance of slow-growing species (van der Sande *et al.* 2016) most likely caused by recovery from past disturbances. Alternatively, drought-tolerant species have been found to increase in abundance in some forest communities (Enquist & Enquist 2011; Feeley *et al.* 2011; Fauset *et al.* 2012). Also, lianas have been found to increase in abundance over the past decades (Laurance *et al.* 2013; Schnitzer 2015). Lianas may be simultaneously better adapted to dry conditions, favoured by disturbances and more

responsive to CO_2-rich conditions than trees (Schnitzer 2005; Körner 2009; Schnitzer & Bongers 2011; Asner & Martin 2012). However the underlying structural and physiological mechanisms are still mostly unresolved (Santiago, Pasquini & De Guzman 2015). Additionally, lianas may decrease tree growth and increase tree mortality, further impacting communities dynamics (Lewis *et al.* 2004; van der Heijden, Powers & Schnitzer 2015).

Permanent plots studies thus paved the way for monitoring changes in tropical forest structure, composition and dynamics, and their limited spatial coverage and temporally discontinuous measurements have been increasingly complemented by continuous and high resolution eddy-covariance flux data (Baldocchi *et al.* 2001; Bonal *et al.* 2008; Restrepo-Coupe *et al.* 2013; Wu *et al.* 2016) and large-scale remote-sensing forest scanning (e.g. Cao *et al.* 2004; Guan *et al.* 2015). Overall, these studies provided additional insights into the drivers of seasonal and inter-annual variations in forest productivity. In most equatorial Amazonia (Restrepo-Coupe *et al.* 2013) and above a threshold of annual rainfall of approximately 2000 mm.yr^{-1} (Guan *et al.* 2015), water limitation was absent and forest productivity variability appeared mostly driven by leaf phenology and incident light radiation (Bonal *et al.* 2008; Wu *et al.* 2016). Below that threshold, water availability was found to strongly constrain forest productivity globally (Cao *et al.* 2004; Guan *et al.* 2015). These results highlighted the potential forests vulnerability to decreasing water availability.

In that respect, recent extreme and exceptional drought events in Amazonia[7] represent natural experiments of a well-identified disturbance. Forest response to these droughts were screened through a diversity of techniques, which overall revealed a decrease in tree growth and an increased in tree mortality. One of the major findings is that, during these droughts, Amazonia has been a transient net carbon source; also, these droughts entailed persistent effects on forest structure and mortality rates (Clark *et al.* 2003; Phillips *et al.* 2009, 2010; Lewis *et al.* 2011; Saatchi *et al.* 2013; Gatti *et al.* 2014; Feldpausch *et al.* 2016). These observations have been supported by long-term throughfall exclusion experiments conducted in Amazonia[8] (Fig. 4), which enable intensive monitoring and thus can offer mechanistic insights into forest response to drought (Nepstad *et al.* 2007; Brando *et al.* 2008; da Costa *et*

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[7] The drought events that occurred in South America resulted from large-scale climatic anomalies, the El Niño Southern Oscillation (e.g. in 1997-1998) and the Pacific Decadal Oscillation and the North Atlantic Oscillation (e.g. 2005 and 2010). These anomalies transitory modified the migration of the Inter-Tropical Convergence Zone on both sides of the Equator, which is a main driver of precipitations over Amazonia.

[8] Ecological studies in the Tapajós (TNF) and Caxiuanã (CAX) National Forests were established in the eastern Brazilian Amazon to directly measure the effects of severe long-term experimental drought on a 1 ha forested ecosystem, by artificially excluding about 50% of incident throughfall by means of large plastic panels disposed just above ground levels.

al. 2010; Metcalfe *et al.* 2010; Meir *et al.* 2015b; Rowland *et al.* 2015). Interestingly, both natural and artificial experiments revealed variability in species vulnerability to drought, leading to contrasting mortality rates. This is in agreement with the idea that past floristic shifts may have been caused by climatic variations.

Other manipulative ecosystem experiments are rare in the tropics (e.g. nutrient fertilization, Tanner *et al.* 1992, Wright *et al.* 2011; fire exclusion, Swaine, Hawthorne & Orgle 1992), but the first free-air CO_2 enrichment (FACE) experiment in the Amazon, the only mean to truly test the debated hypothesis of CO_2 fertilization effect (Körner 2009), is currently being launched (Norby *et al.* 2016).
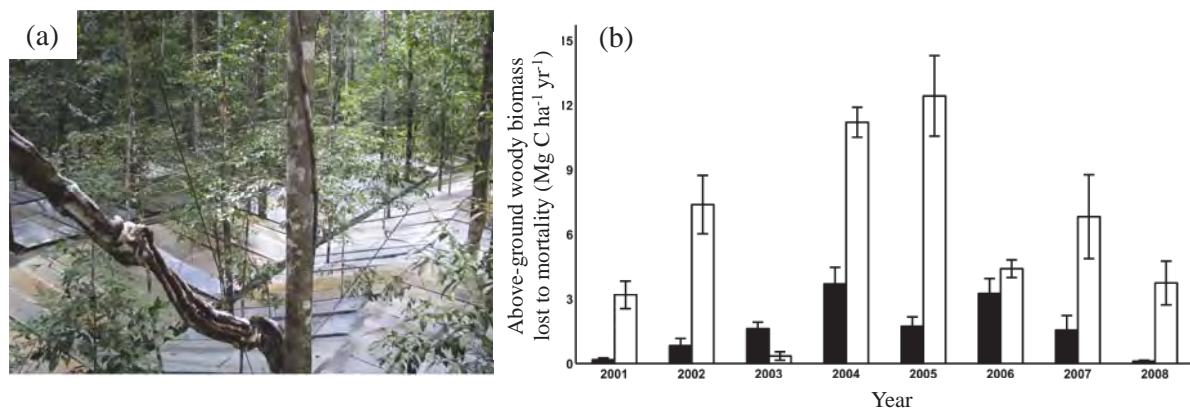
Fig. 4. (a) Large-scale throughfall exclusion experiment in Caxiuanã National Forest, Pará, Brazil. 50% of the incident rainfall is excluded from a 1 ha treatment plot using a system of plastic panels and plastic-lined guttering installed at a height of 1-2 m. From Meir *et al.* 2015b. (b) Annual variation in biomass lost to mortality in the throughfall exclusion experiment in Caxiuana (open bars) and control (closed bars) plots. Error bars: 95% confidence intervals derived from biomass estimates from eight different allometric equations. From da Costa et al. 2010.

In addition to climate change alteration of tropical forests, direct anthropogenic pressures have critically affected tropical forest health and function globally over the past decades (Lewis *et al.* 2015). These pressures are mostly deforestation, mainly for conversion to farmland and mining (Gibbs *et al.* 2010; Hansen *et al.* 2013; Edwards *et al.* 2014a), and forest degradation via hunting, logging, fire and fragmentation and associated edge effects (Laurance *et al.* 2000, 2002; Cochrane 2003; Edwards *et al.* 2014b). The extent of affected forest areas is large. For example, ca. 100 million ha of tropical forest were converted to farmland between 1980 and 2010, corresponding to a rate of 0.4% per year, commonly for soybean or oil palm production (Gibbs *et al.* 2010; Hansen *et al.* 2013). Hunting has led to a decrease in abundance, or even in the extinction[9], of seed dispersers that are vital for forest

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[9] In particular, increasing rarity of large-bodied vertebrates, which dispersed large-seeded trees, raises prices and hence makes it economically attractive to seek out even the last individuals of a species, a phenomenon identified as an "anthropogenic Allee effect" (Courchamp *et al.* 2006). For example, the last Javan rhino in

health and regeneration (Terborgh *et al.* 2008; Harrison *et al.* 2013; Poulsen, Clark & Palmer 2013). All these direct anthropogenic pressures even threat forest health within protected areas (Laurance *et al.* 2012).

    c.   Models to investigate long-term forest response to interacting threats

If critically and fundamentally relying on the basic knowledge developed through field and experimental studies, for their development, calibration and validation, models represent an additional key tool to address unresolved questions on ecosystem long-term responses to global changes.

        Trees are usually long-lived, and experiments and field monitoring should extend over multiple decades to capture long-term trends, a temporal coverage still out of reach of most experimentation. Models are therefore the only option to forecast forest states and dynamics over long timescales. Also, on-going and projected global change has multiple causes, such as temperature, atmospheric chemistry, precipitation regimes, as well as land-use change and fire, which strongly interact with each other and are spatially heterogeneous. The full integration of these factors in site-specific experiments is currently beyond reach. For example throughfall exclusion experiments simulate natural droughts only partially as they do not control for congruent changes in temperature, atmospheric humidity or radiation. Also, CO_2 fertilization may alleviate climate-induced water stress, through an increase in plant water-use efficiency (Brienen, Wanek & Hietz 2010; van der Sleen *et al.* 2015). Models can integrate effects and simulate the complex interplay of hypothesized factors. Besides, in addition to natural and artificial experiments, models can be used to test hypotheses through virtual experiments (e.g. tropical tree physiological isohydry, Fisher *et al.* 2006; tree species richness effect on forest productivity, Morin *et al.* 2011), guide field experiments in a fruitful reciprocal design (Medlyn *et al.* 2015, 2016), and help identify best policy or management interventions, through the definition of alternative scenarios (e.g. forest management, Rüger *et al.* 2007; economic development, IPCC 2013). In that regard, they allow testing alternative relevant trade-off between local and global socio-economic development, ecosystem services maintenance and biodiversity protection.

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mainland Southeast Asia was shot in 2010 and its horn was sold at higher price than gold (Lewis, Edwards & Galbraith 2015).

3. Large uncertainties in model projections of the future of biosphere

a. Towards an Amazonian dieback?

The coupling of vegetation dynamic responses into global climate models (GCMs) (Prentice et al., 2007), together with atmospheric and oceanic processes, has helped forecast the future of vegetation cover in a more informed way. One of the first fully coupled simulations between a GCM and a dynamic global vegetation model (DGVM[10]) has predicted a critical transition of the Amazonian rainforest toward a much drier savannah-type ecosystem under simultaneous sustained deforestation and increase in atmospheric CO_2 concentration (Cox *et al.* 2000, 2004). This scenario, called the "Amazon dieback", has largely contributed to raising awareness on the uncertain future of the largest continuous tropical forest in the world, with paramount implications for humans and wildlife inhabiting this region.

This scenario resulted from positive vegetation-atmosphere feedbacks: the reduced forest cover due to atmospheric warming resulted in a decrease of local evaporative water recycling and a release of CO_2, which, in turn, accelerated global warming and precipitation reduction[11] (Betts *et al.* 2004). This scenario is almost inverse to one of the major evolutionary advance in the history of terrestrial vegetation, under which the rise and ecological dominance of high transpiration functions in angiosperms created the humid conditions that favoured their spatial extent and dominance (Boyce *et al.* 2009, 2010; Feild *et al.* 2011). Similarly, and as first pointed out by Charney (1975), another coupled modelling study confirmed the existence of an alternative "green" state to the current arid state of the Sahara region, both states maintaining a respectively moister or drier climate suited to their persistence, through self-reinforcing mechanisms (Wang & Eltahir 2000; but see also Sepulchre *et al.* 2006)

Several theoretical studies have investigated the tree cover spatial distribution in tropical regions worldwide. They revealed that dense rainforests and savannahs are two alternative stable states in addition to a treeless state, suggesting potential abrupt transitions between them in response to changes in either precipitation or fire regime (Hirota *et al.* 2011;

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[10] DGVMs will be described below in further detail.

[11] Under this fully coupled simulation, CO_2 concentrations were 33% higher and mean land surfaces temperatures 2°C higher by 2100, than in the absence of vegetation-atmosphere interactions.

Staver, Archibald & Levin 2011, Fig. 5). The pattern also indicates a low resilience of systems that reach such tipping points, since the state basins of attraction describe a double hysteresis (Fig. 5). If ecosystems can change gradually, as currently observed in tropical forests permanent field plots, thresholds in external conditions, if reached, may lead apparently stable systems to suddenly tip from one state to another, as has been empirically and theoretically explored for lake eutrophication (Carpenter & Brock 2006; Carpenter *et al.* 2011). Several studies have attempted to identify such thresholds in water availability below which tropical tree functioning and forest state may be critically threatened, and quantified them either in terms of annual precipitations (Guan *et al.* 2015), cumulative water deficit (Malhi *et al.* 2009) or soil extractable water (Meir *et al.* 2015b). These studies all support the non-zero probability of an "Amazonian dieback" transition.
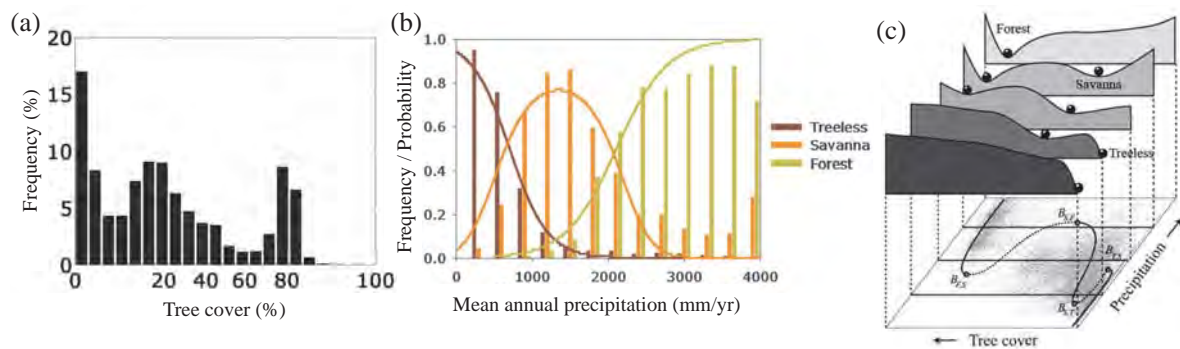
Fig. 5. Tree cover distribution in tropical and subtropical regions of Africa, Australia, and South America. (a) Multi-modal relative frequency distribution of tree cover (T) indicating distinct underlying states: forest, savannah, and treeless, henceforth defined as $T \geq 60\%$, $5\% \leq T < 60\%$, and $T < 5\%$, respectively. (b) The probability of being in each of the states as a function of the mean annual precipitation. Bars represent the relative frequency of the three vegetation types in rainfall classes. Curves represent logistic regression models. (c) The tree cover data (percent, bottom plane) suggest a double catastrophe-fold. Stable states correspond to solid parts of the curve on the bottom plane and to minima in the stability landscapes. Unstable equilibria correspond to the dashed parts of the curve and to hilltops in the stability landscapes. At bifurcation points (B), stable equilibria disappear through collision with unstable equilibria. Resilience measured as the width of the basin of attraction around a stable state diminishes toward such bifurcation points. From Hirota *et al.* 2011.

 b. Data-model inter-comparisons reveal large uncertainties in model projections

Since the seminal study of Cox *et al.* (2000), the "Amazonian dieback" scenario has been largely criticized and reassessed (Malhi *et al.* 2009; Good *et al.* 2013; Huntingford *et al.* 2013). An updated version of the model that first led to this critical transition[12] projected much more limited changes of the Amazonian forest extent for the 21st century (Good *et al.* 2013, Fig. 6). Comparing 22 different coupled models, Huntingford *et al.* (2013) suggested that the positive effect of CO_2 fertilization offset the negative effect of reduced precipitation,

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[12] Respectively the HadGEM2-ES and HadCM3LC models (Fig. 6).

thus leading to a sustained Amazonian carbon sink during the 21st century. However, these projections contradict the observed current decline in the Amazonian carbon sink (Brienen *et al.* 2015, Fig. 3). Also, vegetation models have so far failed to reproduce the impacts of long-term droughts as observed under the Amazonian throughfall exclusion experiments (Galbraith *et al.* 2010; Powell *et al.* 2013; Joetzjer *et al.* 2014). Recently, and comparing several dynamic vegetation models, de Almeida Castanho *et al.* (2016) and Johnson *et al.* (2016) pointed out the inconsistency between models predictions and observed spatial variability in biomass and productivity across Amazonian forests. Such model inter-comparisons have proved useful in identifying processes that lead to data-model discrepancies and that are diversely embedded in different models.
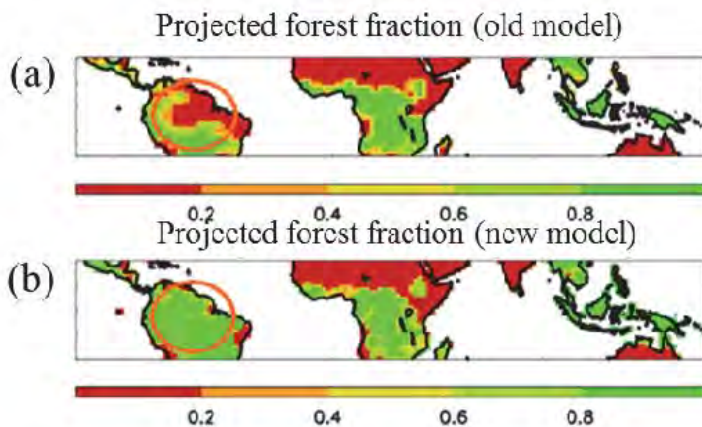
Fig. 6. Forest fraction at the end of the century under the same emission scenario simulated using (a) HadCM3LC that led to an Amazonian dieback, and (b) a more recent version of the model, HadGEM2-ES. From Good *et al.* 2013.

Considering the model-data deviation revealed for present-day simulations, weighted means of future projections across models, with each model's weight being computed from its performance on current time, are often used to cautiously establish most likely scenarios[13] (Malhi *et al.* 2009; Jupp *et al.* 2010; Rammig *et al.* 2010). From the first model inter-comparison study of Cramer *et al.* (2001) to more recent ones (Friedlingstein *et al.* 2013; Friend *et al.* 2014; Sitch *et al.* 2015; Zhang *et al.* 2015), all revealed large discrepancies among model projections for the tropics. Vegetation dynamics and terrestrial ecology has been identified as one of the largest sources of uncertainty in Earth system models (Meir *et al.* 2006; Purves & Pacala 2008; Fisher *et al.* 2014), impairing our ability to provide robust projection of the Earth system.

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[13] Such model inter-comparison exercices are in particular undertaken under standardized scenarios of greenhouse gas emissions within the Coupled Climate–Carbon Cycle Model Intercomparison Project (CMIP), that underlie the reports of the Intergouvernemental Panel on Climate Change (IPCC, http://www.ipcc.ch/).

c. Challenges to build the next generation of tropical forest models.

To improve representation of vegetation and build reliable, robust and realistic[14] forest or land-surface models, modellers have to take up several challenges and include several sources of uncertainties. These can be formalized as follows.

The *epistemic* sources of uncertainty lie in the fragmented and imperfect knowledge we have on plant structure and functioning. Even though plant physiology is an old discipline, important questions on plant responses to environmental cues, such as drought, remain unresolved (see below). Directly resulting from this, the representation of basic processes, such as soil water use or respiration, differ substantially across models, in the absence of a clear consensus on the underlying mechanisms (Galbraith *et al.* 2010). As an illustration, the striking differences between the outcomes of the different versions of the model that first led to the "Amazonian dieback" scenario (Fig. 6), partly resulted from an improvement of our understanding of respiration acclimation to high temperature (Atkin & Tjoelker 2003; Smith & Dukes 2013).

Second, the density and diversity of individual plants in interaction, high in tropical forests, represent a *systemic* challenge, since the whole is not the sum of its parts. Representing the full diversity of plant communities is thus more complex than simulating several monospecific stands in parallel (Porté & Bartelink 2002; Pretzsch, Forrester & Rötzer 2015). For instance, more diverse communities may be more stable and resilient than their less diverse counterparts (May 1973; Yachi & Loreau 1999; Naeem & Wright 2003; Tilman, Reich & Knops 2006). Spatial heterogeneity, both horizontal (e.g. forest gaps, topography) and vertical (e.g. environmental gradients within the canopy) adds up and interacts with this biological complexity (Clark *et al.* 1996; Hubbell *et al.* 1999).

A third *technical* challenge adds up to the other two, and results from the limitations of both biological data and computational power, that have impaired model development. An overarching question that underpins the interaction of these three challenges is the one of the suitable scale to use (Levin 1992; Chave 2013). Should and could each cell, organ, individual, species, population or cohort be represented in a forest model? In each case, what should be the suitable temporal resolution for the simulated process, and what should be the implications for computational requirements? If "the prediction of the ecological causes and consequences of global climate change [requires] the interfacing of phenomena that occur on

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[14] Reliable, robust and realistic: the three R's of next-generation land-surface modelling, as titled by Prentice *et al.* (2015).

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very different scales of space, time, and ecological organisation" (Levin 1992), the answer to these questions may be ascertained on the particular objectives of each modelling enterprise. Under the aforementioned constraints, this may lead to a variety of modelling approaches, defining their proper balance between complexity, realism and generality (Levins 1966; Evans 2012; Evans *et al.* 2013).

II. Modelling tropical forests

1. Historical and disciplinary approaches

In the past, different approaches have been implemented to model tropical forest ecosystem and community dynamics, and also vegetation cover and species distributions. They have been motivated by their own objectives leading to different choices and compromises in their representation of real vegetation. Here I describe three main approaches developed by different disciplines, recognizing that others useful approaches do exist (see e.g. Franklin *et al.* 2016).

a. DGVMs

Dynamic Global Vegetation Models (DGVMs) have been a major advance in simulating global vegetation at the Earth scale. Their major goal was to replace prescribed vegetation states and to thereby improve Global Climate Model (GCMs) predictive power. Since their inception, these DGVMs have been designed to simulate matter and energy fluxes between the vegetation and the atmosphere, including both short- and long-term fluxes. These models have their roots in four different modelling research areas, that were initially investigated separately: plant geography, biogeochemistry, vegetation dynamics and biophysics (Prentice *et al.* 2007; Fisher *et al.* 2014). Describing vegetation dynamics at a global scale inevitably entails strong model assumptions.

The first generation of DGVMs were constituted of a uniform leaf-centred scheme (the so-called 'big leaf' model) that simulated carbon assimilation and evapotranspiration rates as function of climate, typically using a mechanistic framework still widely used in current models (Farquhar, Caemmerer & Berry 1980; Ball, Woodrow & Berry 1987; Leuning 1995; Sellers *et al.* 1997). Leaf-level CO_2 uptake, energy, and water fluxes operate over fast timescales, but through assimilation, they result in slower and broader changes in vegetation structure, composition and function, inducing important feedbacks to climate and long-term

ecological dynamics. These ecological components were later added to DGVMs (Foley *et al.* 1998; Moorcroft 2003; Bonan *et al.* 2003), which thus typically embed several nested time scales (Fig 7). Hourly leaf photosynthetic processes are coupled to a usually daily allocation scheme that drives carbon into different above-ground and below-ground carbon pools, integrating a variety of processes (see Prentice *et al.* 2007 and Fisher *et al.* 2014 for a review). This propagates to longer-term ecological processes such as competition, changes in floristic the composition, structure and fluxes of terrestrial ecosystems.
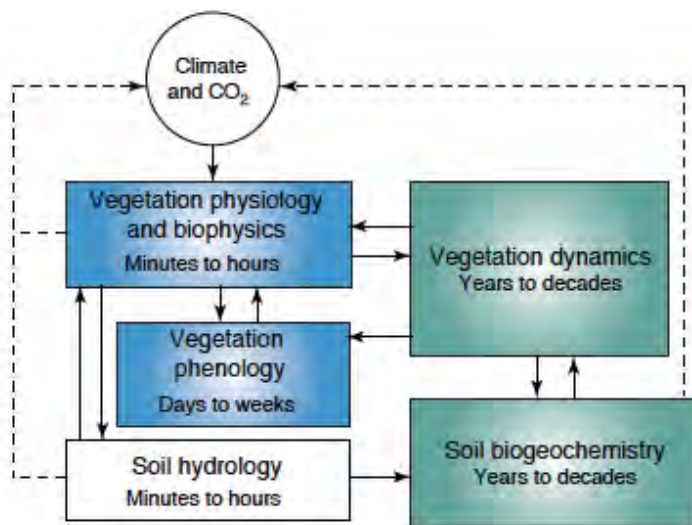
Fig. 7. Typical structure of a DGVM. The first generation of terrestrial biosphere models consisted of a fast-scale leaf photosynthesis scheme that predicted leaf carbon assimilation and evapotranspiration rates as a function of climate, atmospheric CO_2 concentrations, soil hydrological conditions, and leaf physiological traits and phenology (blue boxes). This was then used as a driver of long-term changes in above- and belowground ecosystem structure and composition (green boxes). The dashed arrows indicate the feedbacks between terrestrial ecosystems and the atmosphere captured in these models. From Moorcroft 2006.

Considering the vast diversity of plant species and functions worldwide and the challenge of modelling such processes globally within a tractable computation time, DGVMs make two important assumptions. First, in most DGVMs, terrestrial vegetation biodiversity is aggregated into typically a dozen of discrete plant functional types (PFTs), which are morphological and biogeographical plant groups (see Box 1). A set of fixed properties or parameters is usually assigned to each PFT, and these drive their modelled dynamics. Following this approach, Amazonian plant diversity is considerably simplified into generally one or two PFTs (e.g. Clark et al., 2011; Sitch et al., 2003, see Box 1). The second major assumption is that the environment in which PFTs compete is discretized into ca. $1° \times 1°$ latitude/longitude grid cells, so that plants within each cell typically experience the same averaged abiotic conditions. Consequently, the response of each PFT at the scale of the grid cell is equivalent to an average individual represented by its carbon pools. More complex and finely discretized DGVMs have since build upon these first models, as computational power, knowledge, and biological data are accumulating (Naudts *et al.* 2015).

Box 1. Plant functional types, or how to deal with plant functional diversity in vegetation models?

In DGVMs: a few vegetation types on a global distribution map.
Global vegetation models lump global vegetation diversity into categorical groups, called plant functional types (PFTs). These were originally biogeographical groups that were typically rooted in Köppen's vegetation map and from the heritage of plant biogeography. DGVMs usually include at least five PFTs: broadleaf evergreen trees, broadleaf deciduous trees, needleaf deciduous trees, grass and shrubs. Finer distinctions from these broad groups can be made, for example distinguishing C_3 and C_4 grasses. The total number of PFTs used in current DGVMs is typically 10-20 (Poulter *et al.* 2011; Fisher *et al.* 2014). Within this scheme, tropical tree diversity is generally represented by two PFTs: tropical broadleaf evergreen trees and tropical broadleaf raingreen trees (semi-deciduous vegetation). Tolerance limits regarding bioclimatic variables, such as coldest-month mean temperatures or growing-season heat sums, constrain the climatic area within which each PFT can occur and compete (Harrison *et al.* 2010).

In gap models: a few types along successional and vertical gradients.
Gap models also aggregate temperate and tropical forest species diversity into a limited number of plant functional types. The principles of species aggregation have been widely discussed (Botkin 1975; Lavorel *et al.* 1997), but typically relies on theories that classify plant strategies along ecological performance-persistence trade-offs (Grime 1974). There is no universal classification. However, light being one of the most limiting resource in dense tropical forests, tropical species are often grouped according to their physiological light requirements and tolerance to shade (Swaine & Whitmore 1988; Whitmore 1989), leading to two or three groups, from early-successional 'heliophilic' species to later-stage shade tolerant ones. Another approach has consisted in grouping species by the layer they occupy within the vertical gradient of the canopy (Richards 1936). A combination of both classifications leads to typically 10-20 PFTs within a forest community as simulated by gap models (e.g. Chave 1999; Köhler, Ditzer & Huth 2000). More complex classifications based on species diameter growth trajectories analysis have also been used (Vanclay 1991; Köhler & Huth 1998). All these classifications rely on an important ecological knowledge or amount of field data on the hundreds of tropical tree species typically present within a site. These classifications are not unequivocal and they are difficult to transfer from one site to another (Picard & Franc 2003; Picard *et al.* 2012). The optimal number of PFTs required given a context has also been a matter of debate (Köhler & Huth 1998; Kazmierczak, Wiegand & Huth 2014; Fischer *et al.* 2016).

Using functional traits to group as a continuum.
With the increasing availability of plant functional trait database (see II-2-a) functional traits have been used to generate PFTs at various scales (Hodgson *et al.* 1999; Lavorel *et al.* 2007; Fyllas, Quesada & Lloyd 2012; Verheijen *et al.* 2015). The aim is to simplify the framework and to produce a more relevant and mechanistically-based vegetation classification. However, recognizing that such categorical classifications in discrete group may be arbitrary and overlook a continuous gradient of diverse plant structure and functions, plant traits are also increasingly used to represent plant functions as a continuum rather than as a discrete grouping of plants (see II-2-b).

b. Gap models

Foresters and forest ecologists have developed a long tradition in building growth models, initially to inform forestry management at the stand level with a finer representation of diversity, demographic processes, and spatial constraints (for instance, in logging operations). These models were originally based on simple forest-yield tables, and then led to more complex matrix models (Liang & Picard 2013). Ecological studies of vegetation dynamics (e.g. Watt 1947) then laid the basis of forest simulators that explicitly account for individual tree recruitment, growth and mortality within forest units of the size of a typical gap opening,

hence their name of "gap models". An early example of such a gap model is JABOWA (Botkin, Janak & Wallis 1972). This development has been tightly linked to the development of computational techniques [15] (Bugmann 2001). First conceived to understand forest succession dynamics and productivity, many gap models have considerably expanded this scope (Shugart 1984; Bossel & Krieger 1991; Vanclay 1994; Köhler & Huth 1998) and have been used to address a large number of basic and applied research questions, including forest management or the impact of global changes on long-term forest state (Fischer *et al.* 2016).

The structure of gap models is originally based on the following overarching principles (Bugmann 2001; Porté & Bartelink 2002). Gap models represent individual trees within spatial units called patches, or "gaps". This design was motivated by the recognition that canopy gaps created by the falling of big trees play a foremost role in shaping forest dynamics and structure (Brokaw 1982, 1985; Canham *et al.* 1990). Patch size is set conventionally in these models, as the size of a single dominant canopy tree crown (e.g. 20m×20m), so that environmental conditions within the patch can be considered horizontally homogeneous. This assumption allows tree positions within each patch to be spatially implicit and competition to be assumed equal for all trees within a patch. Patches are not interacting, and their dynamics is therefore simulated independently. Finally, tree leaves are modelled as thin disks at the top of each tree, inducing a strong asymmetrical competition for light among trees differing in their size. Because patches are independent, stand-scale predictions are inferred by averaging over a wide number of independent stochastic simulations, and these simulations can thus be computationally intensive.

Gap models usually implicitly describe the physiological processes of carbon uptake, as opposed to DGVMs. They instead simulate tree growth from empirical equations describing ontogenetic tree trajectory, and infer tree shape and size based on the diameter of trees which is the only state variable measured in forestry surveys. The time scale is either seasonal or yearly. As a result, biogeochemical cycles are usually not fully represented. Gap models were first developed for temperate forests, and mainly focused on commercial species but models of tropical forests were subsequently developed (Bossel & Krieger 1991; Vanclay 1994; Köhler & Huth 1998). These models reproduced forest succession relatively well, by grouping tropical tree species into several PFTs in a need to simplify the high species richness of these forests (see Box 1).

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[15] The development of JABOWA by Daniel Botkin was strongly supported by a collaboration with the IBM Thomas J. Watson Research Center in Yorktown Heights, NY

Because the gap model structure and the consequent assumption of horizontal homogeneity within patches introduce a size bias in competition and have potentially large impacts on recruitment (Porté & Bartelink 2002), several models, among which the first versions of the SORTIE model for a temperate forest (Pacala, Canham & Silander Jr. 1993; Pacala *et al.* 1996) and the TROLL model for a tropical forest (Chave 1999), developed fully spatially explicit and individual-based models. These models keep track of the positions of each tree in a spatially explicit grid, to allow an accurate computation of light conditions for each individual. Other developments have been made from the original gap models (Bugmann 2001; Fischer *et al.* 2016), and other types of models went into finer details of the plant physiology and architecture at much finer temporal scales, simulating processes at the organ- and plant-levels or other fluxes (Williams *et al.* 1996; Le Roux *et al.* 2001; Fourcaud *et al.* 2008; Duursma, Medlyn & others 2012).

Since they describe the fine-grained details of forest growth dynamics and structure, gap models have proved useful in assimilating field data into models and they have evidenced the importance of individual demographic trajectories (Pacala & Deutschman 1995; Moorcroft, Hurtt & Pacala 2001; Smith, Prentice & Sykes 2001; Fisher *et al.* 2010). However, the computationally intensive, data-demanding and stochastic nature of these models have long prevented their use in studying global vegetation-atmosphere interactions, limiting them to the stand scale (Fischer *et al.* 2016). The exponential increase in computer power may open up new perspectives in building spatially-explicit and individual-based model at larger scale, as first proposed by Sato, Itoh & Kohyama (2007). Moorcroft *et al.* (2001) proposed an alternative to up-scale short-term and fine-scale responses of individual plants to long-term and large-scale ecosystem properties and dynamics by using a set of differential equations and a procedure inspired from statistical physics. This approach bypasses the need of numerous and repeated simulations (see also Pacala & Deutschman 1995; Strigul *et al.* 2008).

c. Species distribution models.

At the other extreme of what may *de facto* appear as a biodiversity-ecosystem function modelling trade-off, species distribution models (SDMs) and community models focus on the spatial distribution of species, and their response to environmental factors.

The principle of species distribution models lies on the niche concept, which assumes that species occurrences are determined by biotic and abiotic environmental conditions (e.g.

MacArthur & Levins 1967; Tilman 1980), ignoring demographic stochasticity and historical contingencies (e.g. Hubbell 2001). A niche, as described by Hutchinson (1957), corresponds to a hypervolume in a multivariate environmental space that represents a species environmental limitations. Whether SDMs approximate true species niche has been a matter of debate[16] (Kearney 2006). However the development of a SDM can be described as a two-step process as follows. First, the ecological niche representation of a species is built in an environmental space based on known records (presence/absence or abundance) where environmental conditions have been carefully described. Then each geographic location is assigned a probability of occurrence for the species, based on the niche model (Fig. 8; Elith & Leathwick 2009).
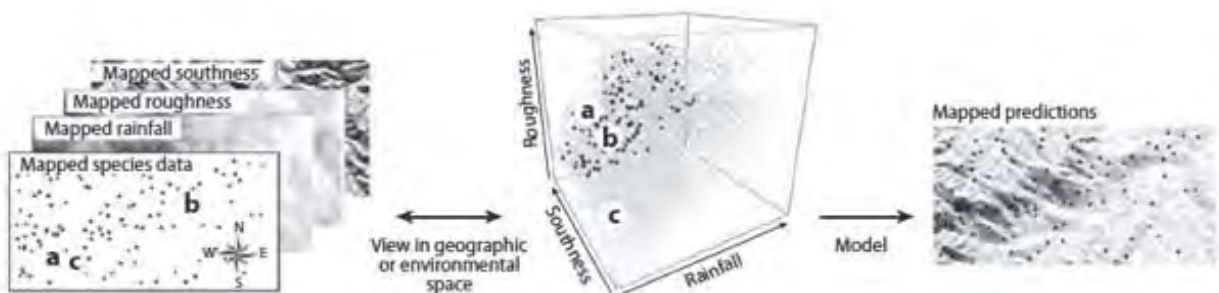
Fig. 8. The relationship between mapped species and environmental data (left), environmental space (center), and mapped predictions from a model only using environmental predictors (right). Note that inter-site distances in geographic space might be quite different from those in environmental space—a and c are close geographically, but not environmentally. The patterning in the predictions reflects the spatial autocorrelation of the environmental predictors. From Elith & Leathwick 2009.

The development and increased adoption of SDMs across a wide array of taxa and environments have relied on several technical progress (Guisan & Thuiller 2005; Elith & Leathwick 2009): new statistical approaches (e.g. MaxEnt; Phillips & Dudík 2008), new methods for physical environment mapping (remote sensing techniques[17]), and increased coordination of effort to compile and increase knowledge on species records (the Global Biodiversity Information Facilities, GBIF[18]), all manipulated together through geographic information systems (GIS). SDMs provide a better understanding and representation of dispersed or sparse species records in species distributions across a landscape, particularly relevant to biodiversity conservation effort (Ferrier 2002). By looking for a best model fit in

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[16] SDMs infer niches from distribution data, so they do not infer the *fundamental* niche, i.e. all environmental conditions where species *could* occur, but the *realized* niche, i.e. the environmental conditions under which species *are actually observed to occur* under additional conditions, such as competition or facilitation.

[17] Tropical Rainfall Measuring Mission (TRMM), http://trmm.gsfc.nasa.gov/

[18] The Global Biodiversity Information Facility (GBIF ; http://www.gbif.org/) is an international biodiversity open data infrastructure, funded by governments. It relate to evidence about more than 1.6 million species (representing hundreds of millions of records) collected over three centuries of natural history exploration and including current observations from citizen scientists, researchers and automated monitoring programmes.

species niche modelling, important key environmental drivers of species spatial patterns may be revealed (e.g. edaphic properties, as in Bertrand, Perez & Gégout 2012). Given the increasing societal demand of a predictive ecology (Mouquet *et al.* 2015), SDMs have been also used to predict species distributions in future environmental conditions, for example in the case of species invasion or migration, or given future climate. However, key assumptions of SDMs, mainly that species are at equilibrium with their environment, may be violated under such applications, preventing trustworthy extrapolations (Svenning & Skov 2004).

SDMs assume little knowledge on the processes from which species distributions result. If this may be an advantage, particularly for poorly known taxa in demand of conservation actions, the integration of processes will likely be critical to infer future distributions under no-present analogue conditions (Kearney & Porter 2009). Models that combine traditional SDMs with process-based information, such as dispersal limitation or phenology, have been developed (Morin, Augspurger & Chuine 2007; Morin, Viner & Chuine 2008; Bykova *et al.* 2012). Also SDMs are limited to a species-by-species approach, and thus overlook species interactions and community assemblage processes, although progress has been made to extend these ideas to full ecological communities (Ferrier & Guisan 2006).

When applied for tree species, SDMs have predominantly dealt with temperate species, because a few dominant species (oak, beech, pine) provide valuable information on the overall forest cover. Tropical tree species have seldom been considered due to their scattered occurrence records (Feeley & Silman 2011a; b), and also because of the difficulty of singling out a few species among thousands. Networks of tropical forest plots have greatly contributed to advancing this field, revealing floristic shift under the influence of climatic and edaphic drivers at the regional scale (Sabatier *et al.* 1997; ter Steege *et al.* 2006; Vincent *et al.* 2011; Quesada *et al.* 2012). Recently, Esquivel-Muelbert *et al.* (2016) have explored the distribution of over 1800 species as a function of water availability from a network of 531 plots across the western Neotropics. They inferred variation in species drought-tolerance (one dimension of their niche) and sought to explain how this resulted in lower community diversity in drier areas, most species being restricted to wetter areas as opposed to the wider range of drought-tolerant species.

2. Bridging the gap among modelling approaches – Towards predictive models of forest dynamics

The challenge of understanding ecosystem functioning and its response to environmental drivers has so far been disconnected from that of biodiversity composition. However they are two facets of ecosystem dynamics and should critically benefit from each other (Mokany *et al.* 2016). Biodiversity influences ecosystem functioning and stability, through species complementarity (Tilman *et al.* 2006; Morin *et al.* 2011, 2014; Loreau & de Mazancourt 2013). Conversely, ecosystem processes and their feedback on abiotic conditions are thought to impact floristic composition. Thus aiming for models that could jointly model fluxes as in DGVMs, demographic processes as in gap models, and species distributions as in SDMs, would be a great advance in this research area (Moorcroft 2006; Purves & Pacala 2008; Mokany *et al.* 2016; Franklin *et al.* 2016). Bridging across these approaches has long been out of reach given the constraints of data and computational power limitations. However, time is ripe for a reassessment of this problem.

a. The promise of plant functional traits

Understanding and predicting species distribution and functioning in their biotic and abiotic environment amounts to solving a fundamental problem in ecology and evolution, which can be formalized by the following integral:

$$I = \int_{E(space,\ time)} f(growth, reproduction, survival)$$

where *E* denotes the environment, which is variable in space and time, and thus the biotic and abiotic constraints, and *f* the species individual fitness or performance, which results from its growth, reproduction and survival abilities. Under this formalism, evolutionary processes tend to maximize *I* under some biophysical constraints (e.g. gravitational constraints on water transport, Woodruff & Meinzer 2011; water metastability under high pressure, Larter *et al.* 2015). Optimization approaches have led to a diverse literature in ecology (Givnish 1988; Anten 2005; Dewar *et al.* 2009; Dybzinski *et al.* 2011; Prentice *et al.* 2014). However,

formalizing *I* explicitly is extremely difficult, notably because identifying measurable determinants of fitness and of its variability is far from obvious.

Darwin (1859) used variation in beak size and shape as a proxy, or *trait*, of resource acquisition in Galapagos finches, i.e. of their organismal performance (*f*), along environmental gradients (*E*), a topic that has been intensively studied since then (Lack 1947; Grant & Grant 2006). Over the past decades, trait-based approaches have been increasingly used in a large number of studies, from organisms of diverse taxa to whole ecosystems (Grime 1974; Petchey & Gaston 2002; Lavorel & Garnier 2002; McGill *et al.* 2006; Toussaint *et al.* 2016). Violle *et al.* (2007) defined a *functional trait* as 'any morphological, physiological or phenological feature *measurable* at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation, which *impacts fitness* indirectly via its effects on growth, reproduction and survival, the three components of individual performance'. The concept of traits thus opens a full research program from measurements in the field, quantifiable values, to individual performance and ultimately ecological patterns at higher levels of organisation such as population, community or ecosystem level. The fact that these traits are repeatedly measureable is thus central and has been a factor of success for trait-based ecology. This is illustrated by the subjective, but revealing, classification of traits into *soft* and *hard* traits, where hard traits capture a function of interest but are difficult or expensive to measure, whereas soft traits are thought to be surrogates of ecological processes but are much easier to measure (Hodgson *et al.* 1999; Weiher *et al.* 1999).

To fulfil the promise of the concept, measured traits must be linked to individual performance, and this has been tested in a large number of studies and traits. Tree growth has been found to be positively associated with both leaf nutrient concentration and adult height, and negatively to wood density, leaf mass per area and seed mass. Mortality rates have been negatively linked to wood density, adult height, seed mass and leaf mass per area (Poorter & Bongers 2006; Poorter *et al.* 2008, 2010; Kraft *et al.* 2010; Hérault *et al.* 2011; Kunstler *et al.* 2016; see Table 1, Fig. 9). The significance of plant functional traits has also been tested at higher levels of organisation. Sets of traits have been found to reveal species abundance dynamics under long-term environmental changes (Soudzilovskaia *et al.* 2013; Li *et al.* 2015), community assembly processes (Ackerly & Cornwell 2007; Kraft, Valencia & Ackerly 2008; Kunstler *et al.* 2012, 2016; Bartlett *et al.* 2015; Fortunel *et al.* 2016), and ecosystem functions (Garnier *et al.* 2004; Cornwell *et al.* 2008; Fortunel *et al.* 2009; Chave *et al.* 2009).

Table 1. Definitions of a few plant functional traits, that are widely used in plant functional ecology. They are relatively easily measured plant characteristics and are thought to play a central role in species strategies to persist in their environment. These traits also play a central role in the definition of plant economic spectra (Wright *et al.* 2004; Chave *et al.* 2009; Díaz *et al.* 2016). Note that these classic traits span leaf, stem and seed organs, but exclude root traits which have been comparatively less explored (Bardgett, Mommer & De Vries 2014; Roumet *et al.* 2016).

Definition	Units	Surrogate of	References
Leaf mass per area	g/cm^2	light interception efficiency vs. leaf persistence	Westoby 1998; Wright *et al.* 2004; Poorter & Bongers 2006; Poorter *et al.* 2009
Nitrogen content per unit leaf mass	g/g	photosynthetic capacity vs. herbivory damage	Wright *et al.* 2004; Poorter & Bongers 2006
Wood density	g/cm^3	mechanical stability and stress tolerance vs. growth potential per investment	Poorter *et al.* 2008; Chave *et al.* 2009; Kraft *et al.* 2010
Adult plant height	m	light acquisition vs. hydraulic constraints	Westoby 1998; Poorter *et al.* 2008; Díaz *et al.* 2016
Seed dry mass	g	establishment success vs. dispersal ability	Westoby 1998; Moles & Westoby 2006; Baraloto & Forget 2007; Poorter *et al.* 2008

However, in most studies, the measured traits (often restricted to a subset of traits of Table 1) explained only a small fraction of the variability in species performance (Poorter *et al.* 2008; Wright *et al.* 2010; Wagner *et al.* 2014, Fig. 9). Paine *et al.* (2015), for instance, found that leaf mass per area, wood density and seed mass together explained only 3.1% of seedling growth variation across 278 species and 27 forest sites worldwide. This poor predictive power calls for consideration of additional, probably *harder*, traits, together with already widely measured traits.
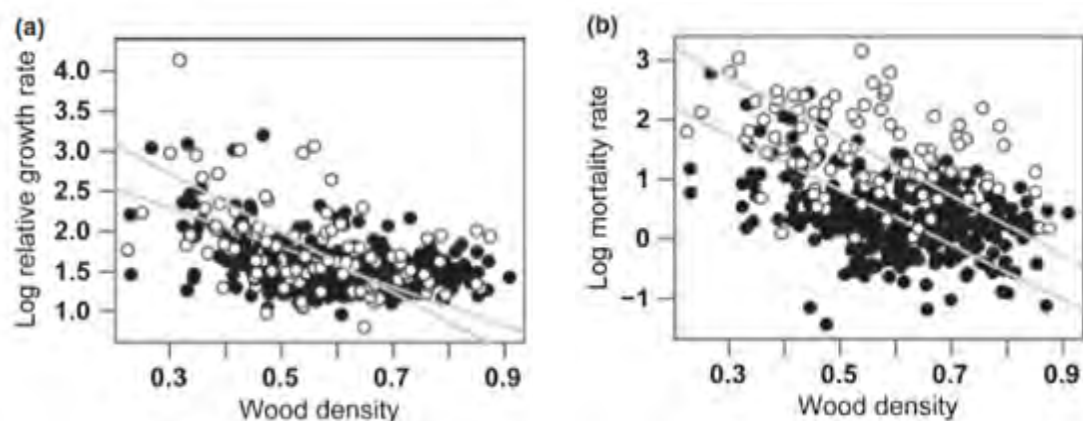
Fig. 9. Relationship between wood density and (a) relative growth rate (log-transformed), and (b) mortality rate (log-transformed), for two tropical forest sites (Barro Colorado Island, Panama, white circles, and Pasoh, Malaysia, black circles). All correlations were highly significant (P < 0.001), and the correlation coefficients ranged between $r^2 = 0.13$ and 0.19. Demographic data were collected from saplings 1–5 cm in diameter under the auspices of the Center for Tropical Forest Science. Drawn from Chave *et al.* 2009.

Global plant trait databases, such as the TRY plant trait database[19] (Kattge *et al.* 2011), has built on important effort of standardization of trait measurement protocols (Cornelissen *et al.* 2003; Sack *et al.* 2010; Pérez-Harguindeguy *et al.* 2013). This effort of compilation has allowed exploration of trait coordination and variation with environment. In a seminal study, Wright *et al.* (2004) showed that, across biomes worldwide, leaf species traits fell onto a single functional multidimensional plane, such that an increase along one axis of performance entails a decrease along another axis. This tradeoff is akin to the equivalent concept in economics, and was therefore coined the *leaf economic spectrum*. It is observed among species within sites, but also across sites regionally or globally. It thus sheds light on a universal trade-off between investment into productive but short-lived leaves with rapid turnover (high nutrient concentration and low leaf mass per area, Table 1, Fig. 10) to less productive but more persistent leaves with longer payback (low nutrient concentration and high leaf mass per area). Using a similar analogy, Chave *et al.* (2009) proposed that wood properties also follow a *wood economic spectrum*, strongly encapsulated by wood density. These leaf and wood axes of variation were found to be uncorrelated (Baraloto *et al.* 2010), such that stem and leaf carbon strategies define a two-dimensional plan in a principal component analysis. Díaz *et al.* (2016) added one trait (seed size, thus using the five traits of Table 1) and found that three-quarter of trait variation across 46,085 vascular plant species worldwide was captured by a two-dimensional global spectrum of plant form and function, thus reducing the number of relevant dimensions of plant trait variation from five to two. The reported coordination among other traits and across a wide variety of biomes and sites (Santiago *et al.* 2004; Meinzer *et al.* 2008; Freschet *et al.* 2010; Patino *et al.* 2012; Mencuccini *et al.* 2015; Roumet *et al.* 2016) led Reich (2014) to postulate that plant operate along a universal "fast-slow" spectrum, embracing plant strategies related to all resources, including water, and all plant organs, including roots.

In light of these functional spectra, it seems that the evolutionary processes that shaped species strategies under environmental and biophysical constraints have considerably restricted the dimensions of the operational space to explore while resolving *I*. Among the infinite variety of shapes and forms, only strategies lying on the emerging axis or plan are allowed to persist. The trait approach provides large datasets of plant performance proxies and reveals trade-off among them. It thus opens new perspectives and facilitates vegetation modelling programs, models being operational integrators (*I*) of individual properties across

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[19] 'The TRY database includes today about 5.6 millions trait records of 100,000 species worldwide and is largely open access' (www.try-db.org),

space and time at the population (SDMs), community (gap models) and ecosystem scale (DGVMs).
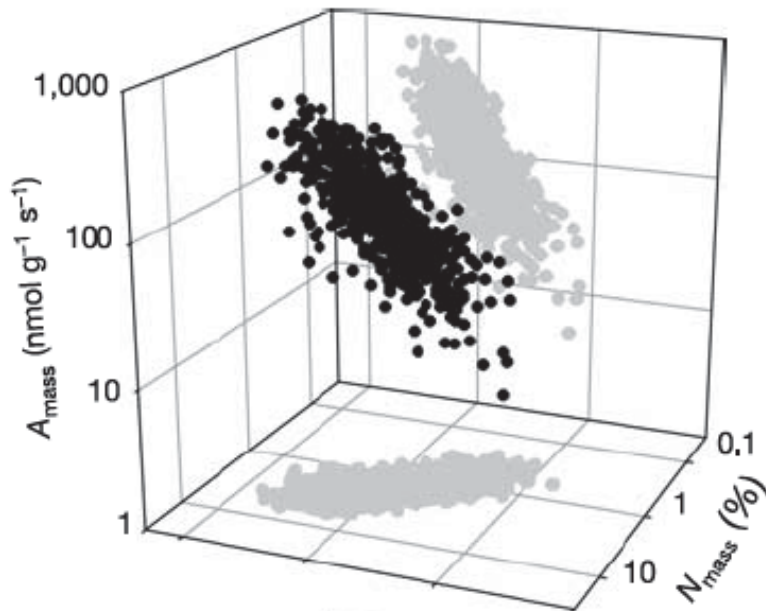
Fig. 10. Co-variation among three key leaf traits in the leaf economics spectrum: LMA, the leaf mass per area; A_{mass}, the photosynthetic assimilation rate measured under high light, ample soil moisture and ambiant CO_2; and N_{mass}, the leaf nitrogen concentration (n=706 species). The direction of the data cloud in three-dimensional space can be ascertained from the shadows projected on the floor and walls of the three-dimensional space. Sample sizes for three-way relationships are necessarily a subset of those for each of the bivariate relationships. From Wright *et al.* 2004.

b. A better functional diversity representation in vegetation models

The crude simplification of plant functional diversity into a few PFTs with fixed mean trait values (see Box 1) overlooks the large spatial variation in key traits within PFTs, which depends on both species and environmental conditions; it also ignores inter-species trait variability within communities as in Amazonia (Fyllas *et al.* 2009; Baraloto *et al.* 2010; Patino *et al.* 2012). A better inclusion of this variability will be necessary to reduce observation-model discrepancies in large-scale modelling (de Almeida Castanho *et al.* 2016). New model approaches have been designed to take advantage of the unprecedented information provided by emerging plant trait databases and to better account for vegetation functional diversity (Van Bodegom *et al.* 2012; Van Bodegom, Douma & Verheijen 2014). Because of the relevance of these approaches to the present study, more details are provided about these recent studies.

Verheijen *et al.* (2013, 2015) allowed some traits to vary within PFTs as a function of climatic conditions in a DGVM, via empirical trait-climate relationships drawn from a large trait database. The explanatory power of such empirical relationships was limited for the traits they considered (leaf mass per area and photosynthetic capacities), particularly so for tropical

evergreen forest. Yet, including these relations resulted in a closer match with natural vegetation patterns. However, they used a single trait value per PFT and per grid cell. Fyllas *et al.* (2014) explicitly modelled a trait continuum in an individual-based vegetation models called TFS (Trait Forest Simulator). Taking advantage of well-documented forest and trait censuses from a network of permanent plots across Amazonia, they allowed each individual to be characterized by its own combination of four traits (leaf mass per area, nitrogen leaf content, phosphorous leaf content, and wood density), drawn from the observed trait combination distribution at each site. They found an improved predictive power for their model compared with a single PFT approach, and concluded on the importance of an accurate parameterisation of within- and across-stand trait variability. However, this approach is data-demanding, requiring site-specific tree diameter and functional traits distributions.

To alleviate this issue of data availability, Scheiter, Langan & Higgins (2013) and Sakschewski *et al.* (2015) (see also Wang *et al.* 2012; Pavlick *et al.* 2013) took advantage of previously published functional trade-offs (Wright *et al.* 2004; Chave *et al.* 2009) to constrain individual trait combinations in their model. They initially attributed trait combinations at random along these functional spectra, and through the modelled processes and resulting environmental filtering, allowed growth strategies to emerge as a response to the biotic and abiotic conditions at each site. They thus avoided the need for *a priori* prescribed bioclimatic limits (e.g. Köppen-Geiger climate classification, Kottek *et al.* 2006) to constrain the range of trait combination or PFTs. Going a step further, Scheiter *et al.* (2013) integrated a genetic optimization algorithm to account for trait heritability between successive generations. In doing so, they thus relax the assumption that the same climate in places with contrasting evolutionary histories, will yield the same response, encapsulated in PFTs' fixed parameters. Even though these approaches are not yet applied at the global scale they are important advances towards DGVMs that better integrate demographic, adaptive dynamics, and functional diversity.

However these approaches may be criticized along two lines of argument. First, they completely ignore species identity, and they are thus taxonomy free. While this may be a welcome simplification in ecosystem science, community ecology and biodiversity challenges are mostly framed in terms of species diversity. Applications of trait-based approaches to integrate mechanistic processes in species distribution models (Kearney & Porter 2009) seem a useful alternative proposal, even though it is currently limited to a few species without interactions. Second, these models rely on documented empirical trait-trait and trait-climate correlations, whose universal relevance remains questionable. The assumption that reported

tradeoffs are consistent across environmental conditions may not be valid. Recently, Asner *et al.* (2016) used airborne imaging spectroscopy to reveal that topo-edaphic conditions strongly modulate purported trait relationships at the canopy level (Fig. 11). The tradeoffs may thus be more variable than usually implied by global analyses (Wright *et al.* 2004). Also, classically used traits (Table 1), almost surely overlook axes of plant variation under global change, especially regarding the tolerance to stress (Craine *et al.* 2012). In spite of the importance of reducing plant traits dimensionality, these studies were restricted to traits related to plant carbon and nutrient economy (Reich 2014). Water functions should be also integrated, and such traits may well add new relevant axes of variation (Laughlin 2014; Li *et al.* 2015a). If so, the poor explanatory power of species performance reported in some studies (Wright *et al.* 2010; Paine *et al.* 2015) may be caused by the studied trait's redundancy, precisely evidenced by the observed spectra, in exploring the whole plant strategies in their variable and stressful environment (Craine *et al.* 2012).
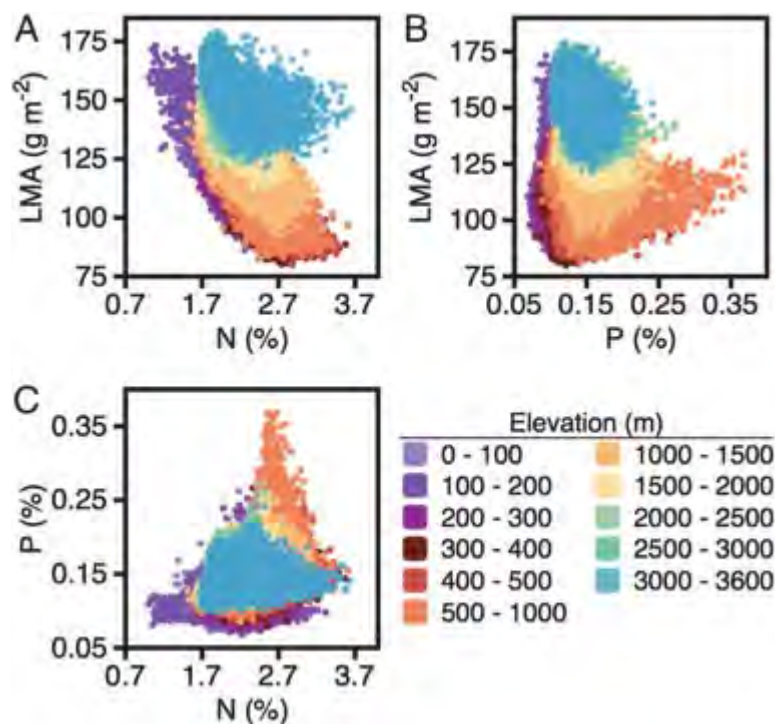
Fig. 11. Relationships between forest canopy foliar N, P, and LMA in discrete elevation bands inferred from airborne imaging spectroscopy, throughout an Andes–Amazon region. Drawn from Asner *et al.* 2016 PNAS.

III. Plant species response to drought

Despite a growing consensus that drought intensity and frequency will increase worldwide in the future (Boisier *et al.* 2015; Touma *et al.* 2015; Duffy *et al.* 2015; Chadwick *et al.* 2016), and the observed vegetation vulnerability to these events (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013; Bennett *et al.* 2015; see above), vegetation response to water stress remains poorly represented in vegetation models (Galbraith *et al.* 2010; Powell *et al.* 2013; Xu *et al.* 2013; Joetzjer *et al.* 2014; Zhang *et al.* 2015). Water-stress induced vegetation responses are diverse and remain understudied. They are thus at the crossroads of the current challenges in global vegetation modelling (Anderegg *et al.* 2013; Meir, Mencuccini & Dewar 2015a; Fatichi, Pappas & Ivanov 2016; Corlett 2016), and this challenge is particularly pressing in tropical forest environments.

1. Plant under drought: a complex cascade of responses.

a. Water flow in a plant.

Water flow in a plant, from soil to atmosphere, is driven by the evaporative demand of water at the leaf surface through stomata (E), which occurs simultaneously to the assimilation of carbon from the atmosphere. This process, called transpiration, can be represented as follows:

$$E = g_S \times A_L \times D \qquad \text{(equ. 1)}$$

where E represents the amount of water transpired by the plant, g_s the stomatal conductance for water vapour, A_L the plant leaf area and D the vapour pressure deficit of the atmosphere, i.e. the water atmospheric demand.

The surface tension at the air–water interface in the leaf causes a strong depression that creates a water potential gradient throughout the plant (see Box 2; Fig. 12). According to the cohesion-tension theory developed to explain the ascent of sap against gravity (Dixon & Joly 1895; Tyree 1997; Angeles *et al.* 2004), water flows upwards in the plant vascular tissue, or xylem, from less negative water potentials in the soil to more negative values in the leaves and in the atmosphere (Fig. 12). The water column remains cohesive owing to hydrogen

bonds that tightly bind water molecules with each other and to the conducting cell walls. Water flow through the xylem can be expressed as follows:

$$J = K \times \Delta\psi = K \times (\psi_{soil} - \psi_{leaf} - \rho g z) \qquad \text{(equ. 2)}$$

where J is the water flow, K the whole-plant conductivity, and $\Delta\psi$ the water potential gradient, in which ψ_{soil} and ψ_{leaf} are the soil and leaf water potentials respectively and $\rho g z$ the gravitational component of the gradient (z being the height of the plant). A plant may thus be seen as a series of hydraulic resistances (the inverse of conductance)

$$K = \frac{1}{R} = \frac{1}{R_{root} + R_{xylem} + R_{leaf}} \qquad \text{(equ. 3)}$$

E (equ. 1) and J (equ. 2) are expressed according to Darcy's law, an analogy of Ohm's law for electrical circuits. Under steady-state conditions, water transport through the xylem (J) balances transpiration losses from leaves (E), and under well-watered conditions, such water flow is driven by the atmospheric demand (D).
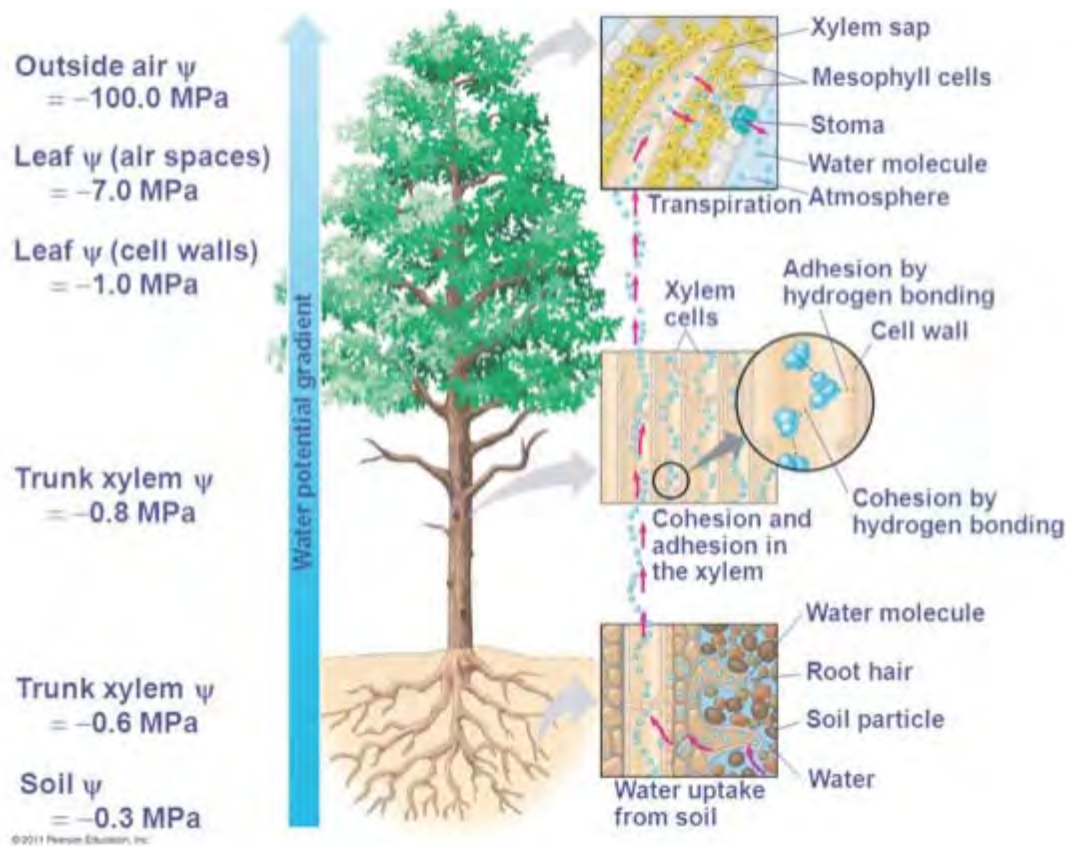
Fig. 12. Scheme of the soil-plant-atmosphere continuum. The water potential gradient is shown with example of water potential values.

Box 2. Water potential: hydric state, tolerance threshold and measurements

Water potential: definition and components.

The water potential is defined as the potential energy of water per unit volume, calculated relatively to that of pure water in reference conditions, and is usually reported in MPa. It quantifies the tendency of water to move from one area to another, due to osmosis, mechanical pressure, or capillary effects, from less to more negative values of potential (Porporato *et al.* 2001; Schulze, Beck & Müller-Hohenstein 2005; Fatichi, Pappas & Ivanov 2016). It is generally determined by the sum of the contributions of these different kinds of potentials:

$$\psi = \psi_M + \psi_G + \psi_P + \psi_S$$

ψ_M is the matric potential, and is due to capillary and adhesion forces, important as the water-solid interfaces. It is thus the major component of soil water potential, and is non-linearly related to the soil water content, through empirical equations depending on soil porosity and texture (Clapp & Hornberger 1978; van Genuchten 1980). ψ_G is the gravitational component of potential which increases with height and equals $\rho g z$, where ρ is the water density, g the gravitational acceleration and z the elevation above a reference level. It thus induces hydraulic constraints on tall trees, leading to an additional xylem tension gradient of ca. 0.01 MPa per additional meter in tree height (Woodruff & Meinzer 2011). ψ_P is the pressure potential, corresponding to the positive pressure of liquid water, for example against cell walls. ψ_S is the osmotic potential, that depends on solute concentration. It equals zero in pure water, and becomes more negative when solute concentration increases.

Leaf water potential: measurements and dynamic under water stress.

The water potential within leaf cells is defined as the sum of two main components, pressure and osmotic potentials. The bulk leaf water potential, ψ_{leaf}, i.e. the volume-weighted average of water potential within the leaf, is typically an indicator of leaf hydration state and demand for water. A more negative ψ_{leaf} indicates a more water-stressed leaf. It can be measured by imposing a positive pressure on the sampled leaf, using a *pressure bomb*, and observing the point when water starts exiting the cut extremity of the twig, corresponding to the equivalent pressure of the negative leaf water pressure or potential (Scholander *et al.* 1964; Tyree & Hammel 1972, Fig.13).
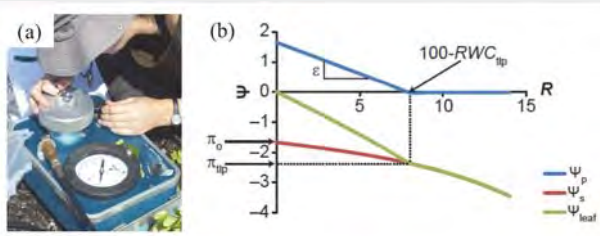
Fig. 13. (a) Measurement of a leaf water potential in the field, using a pressure bomb. The leaf is set within the hermetically closed chamber with the twig or petiole let visible. The pressure within the closed chamber is gradually increased by filling it with gas, until sap is observed to bubble out of the petiole. The reverse of the pressure within the chamber at this point corresponds to the leaf water potential. (b) Plot of water potential as a function of R=100 – total relative water content, in % (pressure-volume curve). From subsequent measurements of the leaf's water potential and its water content, while making the leaf progressively dry out, is drawn a pressure-volume curve. The leaf water potential, ψ_{leaf} in MPa, is the sum of the pressure potential ψ_P and the osmotic potential ψ_S. The y-intercept of the ψ_S curve is the osmotic potential at full turgor (π_o), and when $\psi_P=0$, $\psi_{leaf}=$ the water potential at turgor loss point (π_{tlp}). Drawn from Bartlett, Scoffoni & Sack (2012).

Low negative values of osmotic water potential allow the bulk leaf water potential to remain sufficiently negative to drive water in the cells, while ensuring the pressure potential to be positive, hence maintaining the leaf's healthy state of rigidity, so-called *turgor*. Under water stress, and decreasing leaf water content, ψ_P, and the cells' turgor, decrease, until reaching zero at the so-called *turgor loss point* or *wilting point*, at which the leaf water potential equals its osmotic potential. The more negative the *leaf water potential at turgor loss point* is, the more drought-tolerant is the leaf, since able to sustain rigidity and thus metabolic processes under more negative water potential. This tolerance threshold, as well as other parameters describing leaf responses to water stress, can be deduced by drawing a pressure-volume curve (Fig. 13; Bartlett, Scoffoni & Sack 2012). It is made by progressively dehydrating the leaf in air ("bench dehydration") and regularly measuring its potential and water content (Koide *et al.* 2000; Sack, Pasquet-Kok & PrometheusWiki contributors 2011).

b. Plant functioning under limited water supply

Under limited water supply and as soil moisture content decreases, ψ_{soil} becomes more negative. To sustain J in equ. 2 and hence maintain water transpiration and carbon assimilation, the potential in the leaf as well as the potential in the root and stem all have to decrease, thus putting the plant under increasing water stress. In addition, plant conductivity K is not constant and decreases when the potential decreases, so that:

$$J = K(\psi) \times \Delta\psi \qquad\qquad \text{(equ. 2 bis)}$$

J is thus not proportional to $\Delta\psi$, and this results in a disproportionate increase in the water column tension, due to the decline in conductivity (Sperry *et al.* 1998).

The decrease in plant potential and the increase in the tension of the water column may result in critical threshold being reached. When the leaf water potential reaches the *turgor loss point*, or *wilting point* (Box 2), leaf turgor is lost and the leaf no longer functional, suffering from damages of the photosynthetic machinery, and if the condition persists, the leaf is eventually shed. Also, under increasing xylem tension, an increasing number of *cavitation* events occur. Xylem cavitation corresponds to air-bubbles entering the conductive xylem elements from neighbouring air-filled space or cells. Air then spread into the conduit resulting in *embolism* (Sperry & Tyree 1988; Cochard *et al.* 2009), strongly reducing hydraulic conductance until hydraulic failure (Tyree & Sperry 1989; Sperry & Sullivan 1992).

In order to protect the hydraulic system from such critical failures, plant have evolved a dynamic control system operated by stomata (Jones & Sutherland 1991; McAdam & Brodribb 2012), that act as "pressure regulator" by closing their aperture and thus limit water loss (Sperry *et al.* 2002). The aperture of stomata responds to both atmospheric vapour pressure deficit and soil moisture through a complex array of processes, mediated by hormonal signals (Brodribb & McAdam 2011). By modulating the turgor pressure of the stomatal guard cells that form the stomatal pores, stomata open or close (Buckley 2005).

This control of the plant hydraulic status may be at the cost of reduced carbon assimilation, since CO_2 enters the leaf also through stomata. If stomata are closed for prolonged periods, this may lead to the plant "carbon starvation". Plants usually build reserves to maintain basic metabolic processes during periods of stress, in the form of non-structural carbohydrates (NSC, e.g. starch; Dietze *et al.* 2014)). However, when the stress is too long, NSC stocks may be depleted so that tree health could be seriously compromised (McDowell *et al.* 2008). There has been considerable debate as to whether carbon starvation or hydraulic failure kill tree during drought events (McDowell *et al.* 2008; Sala, Piper & Hoch

2010; Anderegg *et al.* 2012; Hartmann *et al.* 2015; Rowland *et al.* 2015). Drought-induced tree mortality probably results from a complex interaction of carbon starvation and hydraulic failure, together with an increased vulnerability to biotic attacks due to the decline in the overall health status (McDowell 2011; Sevanto *et al.* 2014; Anderegg *et al.* 2015).

Growth may be the first processes to stop under water stress, since cell expansion and division critically rely on cell turgor (Hsiao 1973; Körner 2015; Fatichi *et al.* 2016; but see Doughty *et al.* 2015). Allocation of photoassimilates to the different organs, as well as carbon reserves (NSC), may also change under various stresses (Chen, Yang & Robinson 2013; Doughty *et al.* 2014). Overall, the timing and magnitude of these different plant responses induced by soil drought and increasing atmospheric demand include adjustments at various organisational and time scales and they are currently an active field of research (Fig. 14). This has led to a variety of modelling approaches, at different scales, and through diverse levels of abstraction and assumptions (Fatichi *et al.* 2016).

Process or variables affected	Reduction in tissue water potential ψ and turgor P
	0 ――――――――――――――▷ −2/−12 MPa
Cell growth	
Growth respiration	
ABA release	
Stomatal conductance /transpiration	
Leaf energy budget	
Photosynthesis	
Xylem cavitation	
Root disconnection from soil	
Maintenance respiration	
NSC transport	
Leaf turgor loss	
Leaf shedding	
Plant mortality	
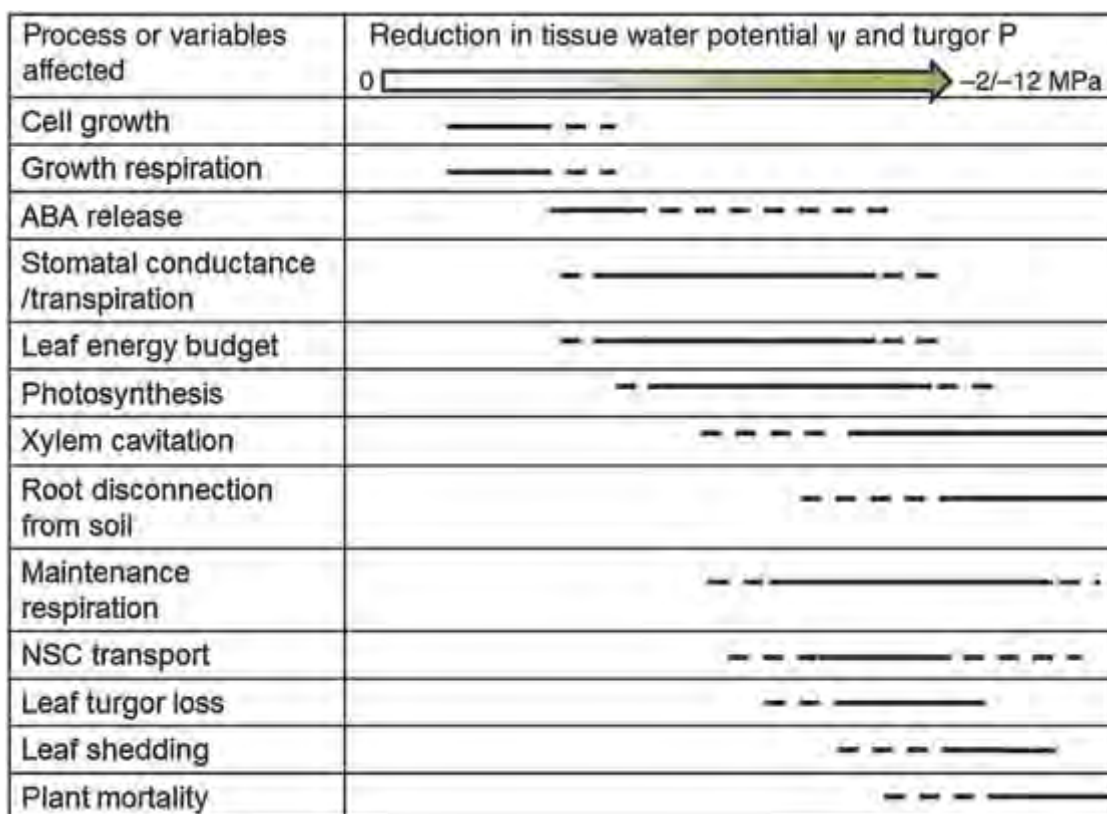
Fig. 14. Effects on plant physiology caused by a decrease in water potential and turgor. The length of the horizontal lines represents the range of stress levels within which a process becomes first affected. Two indicative levels of minimum water potential, Ψ, are given: −2 and −12 MPa. The former is characteristic of drought-intolerant plants/crops and the latter of drought-adapted plants in deserts. Dashed lines signify an incipient or vanishing effect. The relative importance and timing of the different effects remains improperly known. From Fatichi *et al.* 2016, inspired by Hsiao 1973 and Porporato *et al.* 2001.

2. A diversity of strategies of resistance to drought

a. Plants strategies to cope with drought

Attempts have been made to categorize plant species' response according to which process, carbon uptake or water conservation, is favoured, and to sketch alternative strategies of drought tolerance.

A dichotomous classification has been proposed between isohydric species, that prevent a too negative water potential in their water column, and anisohydric species, that tolerate a decrease in this water potential (Tardieu & Simonneau 1998; McDowell *et al.* 2008). Isohydric species would thus respond to water stress by rapidly closing their stomata, in order to limit excessive water loss and maintain high plant potential. In doing so they may prevent excessive cavitation and turgor loss, at the cost of carbon assimilation. They are thus thought to be particularly sensitive to carbon starvation under prolonged drought conditions. Anisohydric species, in contrast, maintain relatively high stomatal conductance, and hence carbon assimilation under water stress, but would take the risk of being strongly water-stressed. There are thus thought to build tissue (xylem conduits, leaves) able to tolerate these stressed states. Under extreme stress, anisohydric species may be more susceptible to hydraulic failure since operating at a low safety margin. The leaf water potential at midday, i.e. when evaporative demand is highest, of anisohydric species thus tracks environmental fluctuations, while isohydric species buffer against these fluctuations (Fig. 15a).
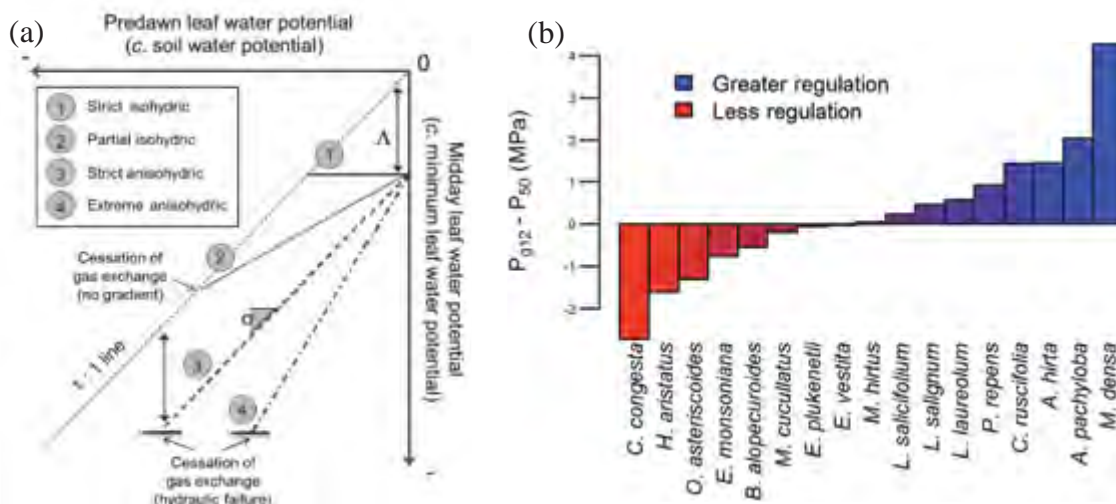
Fig. 15. (a) Relationship between predawn and midday leaf water potentials according to the theoretical framework of Martinez-Vilalta *et al.* (2014), which assumes a linear relationship. Four different behaviours are depicted, all sharing the same intercept (Λ): strict isohydric (r = 0), partial isohydric (0 < r < 1), strict anisohydric (r = 1) and extreme anisohydric (r > 1). The point of cessation of gas exchange is also represented: for isohydric behaviours, it occurs when the predawn water potential equals the midday water potential; for anisohydric relationships, it occurs when the midday water potential reaches the water potential inducing complete loss of plant hydraulic conductance. The 1 : 1 line is also depicted. From Martinez-Vilalta *et al.* 2014. (b) Stomatal safety margin ($P_{g12} - P_{50}$) of species from mountain fynbos in South Africa's Cape Floristic Region, showing the range of stomatal regulation strategies within a single community. Skelton *et al.* (2015) suggest that $P_{g12} - P_{50}$ provides a proxy for degree of isohydry/anisohydry, where P_{g12} is a proxy of the point at stomatal closure and P_{50} quantifies the vulnerability to cavitation. From Skelton et al. 2015.

However, such a dichotomous classification arose from studies on ecosystems with few codominant species, exhibiting contrasting strategies (e.g. piñon–juniper woodland; McDowell *et al.* 2008; West *et al.* 2008). More recent studies suggest that woody plant species actually draw a continuum between these two extreme strategies (Martínez-Vilalta *et al.* 2014; Klein 2014; Skelton, West & Dawson 2015, Fig. 15b). Also some species have developed alternative mechanisms to cope with drought (Fig. 16, Delzon 2015). Some plants may invest into developing a deep root system to access deep soil water and thus escape the drying superficial soil layers (West *et al.* 2012), being thus "drought avoiders", but also "water spenders" as opposed to typical isohydric species that are more "water savers". Also, deciduous species escape drought by shedding their leaves annually, while potentially sustaining a minimal carbon assimilation rate through the development of a photosynthetic stem (Pivovaroff *et al.* 2016). Considering the variety of mechanisms developed to cope with droughts, the mere existence of clear categories of hydraulic response to drought and drought tolerance is currently a major controversy in plant hydraulics (Sack *et al.* 2016).

Drought resistance

Escape

Phenology
(e.g. annual plant
ephemerophytes)

Exposure to stress

Avoidance

(Homeostasis in midday
leaf water potential)

- Water savers
stomatal regulation
water storage
(e.g. *Pinus* sp.)

- Water spenders
deep root system
(e.g. *Prosopis* sp.)

Tolerance

(Drop in midday leaf
water potential)

- Xylem resistance to
cavitation
(e.g. *Callitris tuberculata*)

- Turgor loss point
(e.g. *Acacia greggii*)

Fig. 16. Alternative strategies for plant survival to drought. Escape is defined as a temporal absence during the drought period, due to the shedding of leaves, as in ephemerophytes. Avoidance is the minimization of water loss in plants experiencing drought or an increase in water uptake, through better stomatal control or a greater investment in the below-ground biomass, respectively. The midday leaf water potential is therefore maintained relatively constant despite fluctuations in soil water content. Tolerance involves mechanisms allowing plants to survive dehydration by constructing xylem conduits more resistant to cavitation and implosion and/or by having a more negative turgor loss point, corresponding to the water potential at which leaf cells lose turgor (leaf wilting). *Callitris tuberculata* is the species with the highest level of cavitation resistance ever measured (-18.8 MPa, Larter *et al.* 2015), whereas *Acacia greggii* is the species with the most negative leaf turgor loss point (-4.25 MPa, Bartlett, Scoffoni & Sack 2012). Those species can thus withstand low water potentials. Redrawn from Delzon *et al.* 2015.

b. Strategies of plant resistance to drought vary widely across species within communities

Water availability has constrained evolution of plant structure and functions across biogeographical gradients (Brodribb & Hill 1999; Augusto *et al.* 2014; Klein, Randin & Körner 2015). Species sensitivity to drought has thus been found to strongly underlie their distributions regionally (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008; Condit *et al.* 2013; Esquivel-Muelbert *et al.* 2016). As a result, woody plants from a wide range of biomes tend to display similar susceptibilities to drought, as revealed by their safety margin, computed by the difference between the minimal water potential typically experienced by the plants in its environment and the potential inducing 50% loss of hydraulic conductance induced by cavitation (P_{50}, in MPa; Choat *et al.* 2012). This global compilation has revealed that species are finely tuned to the environmental conditions they strive in (Choat et al. 2012), but it also

raised awareness on a global convergence of species vulnerability to a future increase in drought intensity worldwide.
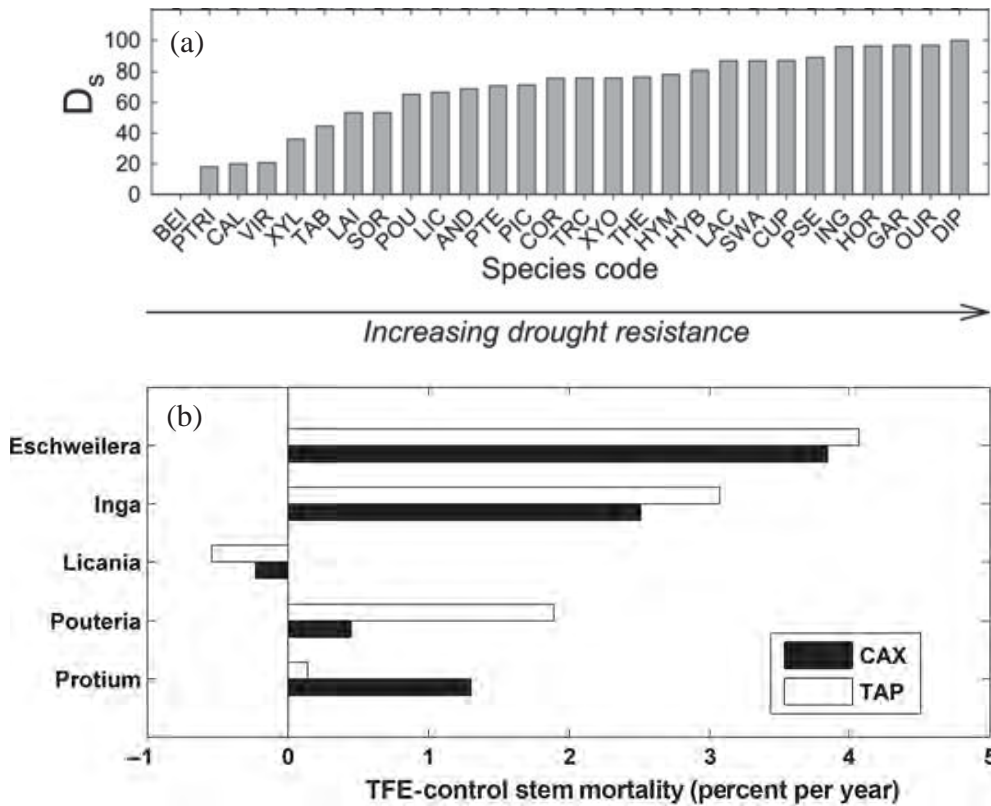
Fig. 17. (a) Survival in a dry treatment relative to the wet treatment ($D_S = S_D / S_W \times 100$, where S_W and S_D are the numbers of seedlings after 22 weeks relative to the sample size at the beginning in the wet and the dry treatment respectively) for 28 tropical woody species co-occuring at the same site in Panama. Species are sorted by increasing rank of drought resistance. From Engelbrecht & Kursar 2003. (b) The absolute difference in mortality response to throughfall exclusion experiment for trees (≥ 10 cm diameter at breast height) of five of the most common genera. Data from Caxiuanã National Forest (CAX) and Tapajós National Forest (TAP), Brazil. From Meir *et al.* 2015b.

However, such patterns also hide considerable diversity in drought resistance within plant communities (Engelbrecht & Kursar 2003; West *et al.* 2012; Craine *et al.* 2013; Salgado Negret *et al.* 2013; Pivovaroff *et al.* 2016). Engelbrecht & Kursar (2003) explored the vulnerability to drought of 28 tropical woody species occurring at the same site, by imposing a drought treatment on seedlings in a greenhouse experiment. They found a wide variability in the species resistance to drought: vulnerable species exhibited a survival rate under the drought treatment about five times lower than in control conditions, whereas resistant species exhibited almost no differences (Fig. 17a). This diversity of vulnerability to drought within a single forest type was also observed on mature trees in the field under both artificial

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throughfall exclusion experiments (Fig. 17b; Meir *et al.* 2015b) and for natural extreme drought events (Phillips *et al.* 2010).

3. Drought-tolerance traits

Considering the wide diversity of strategies to cope with water stress, it is important to quantify them through standardized measurements of functional traits across individuals and species within and across biomes, so as to better understand and model vegetation responses to drought. However, the identification of the traits that influence the most plant performance and survival under drought, remains debated (Sack *et al.* 2016).

In the past, leaf mass per area and wood density have been proposed as practical proxies of leaf and stem resistance to drought, respectively (Niinemets 2001; Hacke *et al.* 2001; Lamont, Groom & Cowling 2002; Santiago *et al.* 2004). This was based on the reasoning that thick leaves tend to dominate dry floras and that dry-forest trees also tend to have a denser wood (Chave *et al.* 2006). However, such structural traits are also directly related to a myriad of constraints such as light levels, nutrient availability, intensity of herbivory or mechanical constraints (Poorter *et al.* 2009; Zieminska *et al.* 2013; Fortunel *et al.* 2014). Consequently, they have been shown to be poor predictor of drought-tolerance (Blackman, Brodribb & Jordan 2010; Bartlett, Scoffoni & Sack 2012b). Leaf water potential at midday, or minimal leaf water potential, has often been used to reveal the typical hydric stress state experienced by a plant and thus the level of stress it is able to tolerate. However, this water potential at midday defines a hydric state, and does not inform underlying mechanisms. Also it does not provide a robust proxy of hydraulic failure thresholds.

Three such thresholds are often used in the literature: the potential at leaf turgor loss point (π_{tlp}, in MPa), and the potential inducing 50% or 88% loss of xylem conductance (P_{50} and P_{88}, in MPa). P_{50} and P_{88} have been identified as thresholds for recovery failure for gymnosperms (Brodribb & Cochard 2009; Brodribb *et al.* 2010) and angiosperms (Urli *et al.* 2013), respectively. The variation in P_{50} and π_{tlp} among species has been associated with spatial variability in water availability within and across biomes (Brodribb & Hill 1999; Maherali, Pockman & Jackson 2004; Lenz, Wright & Westoby 2006; Baltzer *et al.* 2008; Bartlett, Scoffoni & Sack 2012b; Choat *et al.* 2012; Fig. 18). In addition, it has been repeatedly emphasized that both traits underlie plant performance and survival under water stress (Baltzer *et al.* 2008; Brodribb *et al.* 2010; Urli *et al.* 2013; Anderegg *et al.* 2016).

However, these drought-tolerance traits are time-consuming to measure, as they are based on the construction of full leaf pressure-volume curves (Box 2) or xylem vulnerability curves. Also, various methods developed to construct xylem vulnerability curves are prone to biases and artefacts. There is thus an active debate about which method to be used as a benchmark (Cochard *et al.* 2013; Sack *et al.* 2016). In particular, tropical tree species that have particularly long-vessels may be susceptible to the open-vessel artefact of some methods (Sperry *et al.* 2012; Martin-StPaul *et al.* 2014; Torres-Ruiz *et al.* 2014; Delzon 2015). The development of widely applicable and robust methods to measure vulnerability to cavitation is still an active area of research (Choat *et al.* 2015; Pereira *et al.* 2016).

Consequently, few data for P_{50} and π_{tlp} exist for tropical tree species. Two global meta-analyses of P_{50} (Choat *et al.* 2012) and π_{tlp} (Bartlett *et al.* 2012b) has been made recently. For P_{50}, Choat *et al.* (2012) reported data on 75 tropical rainforest species out of 480 in their compilation (none for Amazonia), while for π_{tlp}, Bartlett *et al.* (2012b) reported data on 50 tropical rainforest species out of 317 species (four for Amazonia). This reveals biases in data availability both against tropical rainforests relatively to their species diversity across biomes, and towards a few sites in Central America and Asia for rainforests.
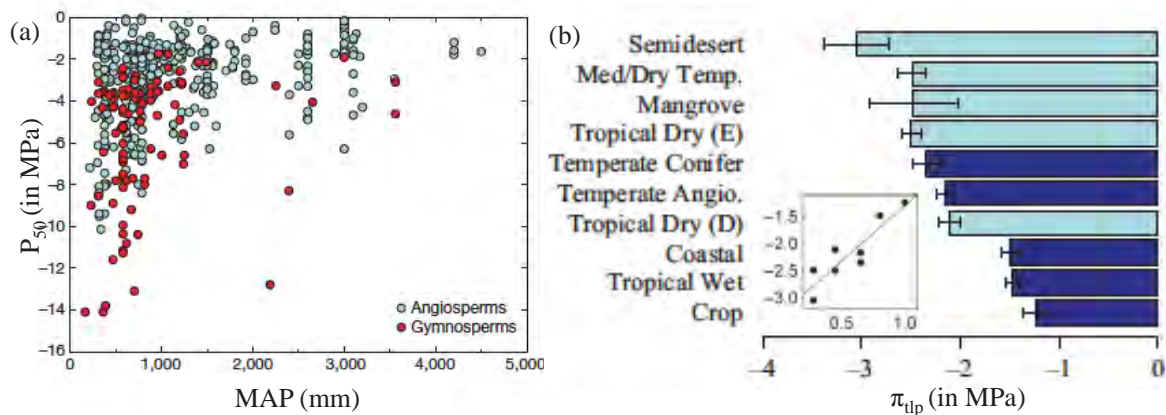
Fig. 18. (a) Embolism resistance as a function of mean annual precipitation for 384 angiosperm and 96 gymnosperm species. Each point represents one species. A generalized model indicated that embolism resistance (P_{50}, in MPa) was significantly related (p<0.00001) to mean annual precipitation (MAP, in mm) for angiosperms and gymnosperms, with decreasing resistance to embolism corresponding to increasing rainfall. From Choat *et al.* 2012. (b) Global data for leaf water potential at turgor loss point (π_{tlp}, in MPa, with mean ± standard error) across biome categories, with inset plots of biome category means against the Priestley–Taylor coefficient of annual moisture availability α. Data within biomes were separated into evergreen (E) vs. deciduous (D) when significantly different. π_{tlp} showed separation of moist and dry biomes (light and dark blue bars respectively), and correlated with α across biomes ($r^2 = 0.81$, p = 0.006). From Bartlett *et al.* 2012b.

Also, it has often been hypothesized that the safety of the xylem should trade-off against xylem efficiency, because of structural and evolutionary constraints. Hence the ability to resist to embolism formation and spread, as measured by a well negative P_{50} value (safety),

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should trade-off against the capacity to transport water, as measured by high xylem conductivity (efficiency). If so, P_{50} should be a suitable proxy for hydraulic syndromes. However a recent global meta-analysis reported only a weak trade-off between xylem safety and efficiency across more than 400 species of angiosperms and gymnosperms (Gleason *et al.* 2016b). In particular, many species displayed a low efficiency and also a low safety. Reasons underlying these unexpected results are unknown and are still being debated (Gleason *et al.* 2016a; Bittencourt, Pereira & Oliveira 2016). Additional functional traits would be required to better measure plant efficiency and to better understand the range of hydraulic strategies, especially including coordination with leaf and root traits (Brodersen 2016). For example, sapwood capacitance, deciduousness, root depth, cuticular conductance, photosynthetic stem or leaf area-to-sapwood area ratio may all help characterize the diversity of plant hydraulic strategies (Meinzer *et al.* 2009, 2010; Pivovaroff *et al.* 2016).

In an attempt to build a standardized method to quantify whole plant hydraulic strategies, Martínez-Vilalta *et al.* (2014) proposed a theoretical framework describing plant responses to drying soil, based on the relationship between time series of midday and predawn leaf water potentials (Fig. 15a). The predawn leaf water potential, measured at the end of the night, is indeed often used as a proxy of soil water potential in the plant root zone, under the assumption that plant and soil water potentials equilibrate overnight[20]. Martínez-Vilalta *et al.* (2014) used the parameters of this relationship (intercept and slope) to inform transpiration rate as a function of water transport efficiency and their sensitivity to soil drought. They applied this framework for 102 species and found significant associations of these parameters with climate. In doing so, they aimed at capturing the whole plant response, since changes in the gradient of the plant water potential result from both the sensitivity of transpiration rate to drought, i.e. the stomatal control, and changes in the hydraulic pathway conductance. Going a step further, Skelton *et al.* (2015) moved from the commonly used safety margin between midday leaf water potential and P_{50} (Choat *et al.* 2012), to propose a new standardized safety margin defined as the difference between the leaf water potential at stomatal closure and P_{50} (Fig. 15b). In doing so, they aimed at explicitly quantifying the relative strength of stomatal control and conductivity loss in shaping the various responses to drought. One limitation of Martínez-Vilalta *et al.* (2014) and Skelton *et al.* (2015)'s approaches is that numerous field measurements are needed. They either required numerous subsequent measurements of midday and predawn water potentials, or the generation of

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[20] This assumption may not always be valid (Donovan, Linton & Richards 2001).

whole vulnerability curves. This is impractical on canopy trees, given limited access to leaves and the large local species diversity of tropical forest trees.

In the face of the controversies and technical challenges, a practical hydraulic trait-based framework is yet to be proposed and adopted (Sack *et al.* 2016). It should be suited to tropical tree species structure and diversity, and thus permit the study of tropical forest vulnerability to drought at the community level. Such research challenge will require further explorations based on integrative and collaborative approaches between experiments, observations, measurements and models (McDowell *et al.* 2013; Sack *et al.* 2016).

IV. Objectives and approaches

1. Objectives

Although they play a crucial role in the global climate, they shelter large biodiversity, and they provide numerous ecosystem services, the future of tropical forests is uncertain. Direct anthropogenic pressures and on-going climate change currently threat their health. In particular, the predicted increase in drought intensity and frequency may impact forest structure and composition, and their vulnerability has already been observed in natural and artificial experiments.

To understand and predict forest responses, different modelling approaches have been developed by different disciplines, with different objectives and assumptions. Dynamic global vegetation models focus exclusively on ecosystem functions and simplify global vegetation structure and diversity in an extreme manner. Gap models use a finer description of forest structure and diversity, still aggregating plants in discrete groups, but with a finer resolution. They however produce an incomplete sketch of ecosystem functioning. Species distribution models describe and predict species distributions in a spatially-explicit environment at the landscape scale, species by species. They thus use a finer taxonomic description, but overlook vegetation properties at the scale of community and ecosystem. The different assumptions made by these different modelling approaches were essentially constrained by data and computational limitations, which are strong in regard to the complex ecophysiological processes and large diversity involved.

However, the exponential increase of computational power and data availability open new perspectives to alleviate these limitations. In particular, functional traits help quantify individual features that underlie plant performance and survival in a variable environment. They also help upscale plant organ and individual properties at the population, community and ecosystem levels. The trait-based approach thus paves the way to jointly simulate ecosystem functions and biodiversity composition, which is desirable considering the tight connections between these two facets of ecosystem dynamics. However, finding measurable traits that are tightly link to plant fitness is a complex research program. This is particularly

the case for hydraulic and drought-tolerance traits, as plant strategies of response to drought are complex and diverse.

The overarching goal of this thesis was to contribute to a better understanding of tropical forest dynamics, through empirical and modelling approaches, taking into account the wide functional and species diversity that these ecosystems shelter. This work lies at the interface between modelling and ecophysiology as it uses both approaches. The modelling approach developed here seeks to jointly simulate ecosystem function and structure and biodiversity composition. It makes use of increasingly available information on plant functional traits. Considering the lack of data on drought-tolerance traits in tropical forest communities, drought-tolerance was also quantified in the field, using novel techniques that are adapted to tropical forest species and their large diversity.

2. Outline

In **Chapter 1**, a new tropical forest simulator is described, developed to simultaneously simulate carbon and tree species diversity dynamics. It is a spatially-explicit and individual-based model, hence able to explicitly represent demographic dynamics in an heterogeneous environment. This dynamics results from physiological processes explicitly integrated in the model, and whose parameters are species-specific. It thus keeps track of species identity and simulates community assemblage. During this thesis project model development was made from the TROLL model (Chave 1999). In its original version, TROLL missed most of the physiological mechanisms and species-level parameterization. Since then, the increase in data availability, among which a species functional trait database (Baraloto *et al.* 2010a), has allowed the representation of tree diversity at the species level, while integrating processes underlying plant competition and responses to environment in a more mechanistic way. This development seeks to integrate an active research literature in tropical tree ecophysiology. A model simulation of forest regeneration from bare-soil, parameterized with data from tropical forests in French Guiana, is validated against various and independent field datasets from both an early forest regeneration and mature forest plots (**Chapter 1**).

Considering the lack of both knowledge and data informing tropical tree species responses to drought, hydraulic responses were not explicitly represented in this version of the

TROLL model. Consequently, in the following chapters, the drought tolerance diversity was quantified within an Amazonian forest community, as revealed by the leaf water potential at turgor loss point (π_{tlp}, Box 2). This work has benefited from the recent development of a new standardized method, much more rapid than the commonly used time-consuming pressure-volume curve method (Bartlett *et al.* 2012a). It thus allows to consider measuring π_{tlp} at the community level. Using this method, the first community-level assessment of the diversity of such a *hard* drought-tolerance trait in an Amazonian rainforest is presented, spanning 165 trees of 71 species, at three sites within forests in French Guiana (**Chapter 2**). An independent validation of the method and a deeper exploration of π_{tlp} intra-specific and seasonal variability on a subset of species at our sites are then reported (**Chapter 3**). Finally, a focus is made on differences between lianas and trees with respect to π_{tlp} across seasons (**Chapter 4**).

Overall, π_{tlp} may be a good candidate to help parameterize plant responses to drought in vegetation models. In **Chapter 5,** the link between π_{tlp} values and whole plant response to drying conditions is explored. Diverse tree sensitivities to drying conditions in the field, as measured by sap flow variation of mature trees during a marked dry season, are compared to their contrasting π_{tlp} values (**Chapter 5**). As sap flow variation includes both leaf and stem responses to drought, and to further explore the integration of drought-tolerance at the whole plant scale, π_{tlp} and P_{50} values were also compared in a compilation of tropical plant species. Trait values and tree dynamic responses used in Chapters 2 to 5 were measured during field missions organized and designed as part of this PhD project, in both Nouragues and Paracou research station, French Guiana.

Finally, in the discussion, I provide a synthesis of the results of the different chapters, and discuss the perspectives that emerge from this study.

3. Study sites

All data used as part of this work have been collected in French Guiana's rainforests. French Guiana is the only French and European territory located in South America. More than 95% of its ca. 84,000 km^2 is covered by a dense rainforest ecosystem, barely perturbed by human activities, which mostly concentrate on a thin coastal zone. It is part of unique geological unit, the Guiana Shield, which spans from the East of Colombia to Amapa State of Brazil, including Suriname, Guyana, French Guiana, as well as parts of Venezuela. Forests of the Guiana Shield grow on old crystalline substrates (Quesada *et al.* 2010), are known to present a particularly high biomass and a low mortality rate (Johnson *et al.* 2016), and a tall canopy of typically 20-45m, with some emerging trees reaching 50-60m (Feldpausch *et al.* 2011), compared with the rest of Amazonian forests. They also have a distinct species composition, dominated by Fabaceae, Burseraceae, Lecythidaceae and Chrysobalanaceae (ter Steege *et al.* 2006).

Most data used in this contribution were collected in the Nouragues Ecological Research Station[21] and in the Paracou Research Station[22] (Fig. 19), in which permanent plots have been progressively intensively monitored since 1986. The Nouragues Ecological Research Station is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05'N, 52°40'W; Bongers *et al.* 2001). The bedrock is varied at this site: the majority of the forest grows on metamorphic bedrock of the Paramaca series, covered with clay soil, while a smaller area surrounding the granitic outcrop has granitic and crystalline bedrocks covered with soil with a mixture of clay and sand derived from the bedrock (Grimaldi & Riéra 2001). The Paracou Research Station is located close to the village of Sinnamary and 20 km from the coast (5°15'N, 52°55'W; Gourlet-Fleury, Guehl & Laroussinie 2004). The bedrock is a metamorphic formation of the Precambrian Shield, dominated by schists and sandstones. Soils are limited in depth by a lateritic pan, which has a low permeability and leads to lateral drainage during heavy rains (Ferry *et al.* 2010).

Permanents plots are regularly censused in both stations. Litterfall traps also enable to follow litterfall productivity and seasonal and long-term dynamics. Meteorological stations inform the climate variability with a half-hourly time resolution. An eddyflux tower, *Guyaflux*, was settled in the Paracou station in 2003, to measure gas exchanges between the

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[21] http://www.nouragues.cnrs.fr/
[22] http://paracou.cirad.fr/

canopy and the atmosphere in situ at high time resolution (Bonal *et al.* 2008). Another eddyflux tower, *Nouraflux*, has been recently settled in the Nouragues station.

Fig. 19. Map of French Guiana, with locations of the Nouragues and Paracou research stations.

Temperature is quite stable at these sites, around 26°C, and rainfall presents significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. Despite some variations and a gradient in annual rainfall across French Guiana, both sites receive c.a. 3000 mm/yr rainfall, with a long wet season from December to July, often interrupted by a short dry period in March. The dry season typically lasts from the end of August to November with 2-3 months with precipitation <100 mm/mo (Bongers *et al.* 2001).

These two sites were part of a functional trait census[23] (Baraloto *et al.* 2010a), that included nine 1-ha plots distributed across French Guiana. All trees with a diameter at breast height >10cm were mapped and identified and measured for about 10 leaf and stem functional traits, including leaf mass per area, leaf nitrogen concentrations and wood density. Overall, 4709 individuals representing 728 species were sampled as part of this project.

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[23] http://www.ecofog.gf/bridge/index.html

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Joint simulation of carbon and tree diversity in an Amazonian forest with an individual-based forest model

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Chapter outline

Jointly simulating ecosystem functions and biodiversity composition is desirable considering the tight connections between these two facets of ecosystem dynamics. Individual-based models constitute a natural approach to account for vegetation diversity and demographic dynamics in an heterogeneous environment, while taking advantage of diverse data available at a range of scales, from organ and individual scales to stand scale. In this **Chapter 1**, a new individual-based, spatially-explicit and trait-based tropical forest simulator is described, developed to simultaneously simulate carbon and tree species diversity dynamics. A model simulation of forest regeneration from bare-soil, parameterized with data from tropical forests in French Guiana, is validated against various and independent field datasets from both an early forest regeneration and mature forest plots. The model sensitivity to a number of key global parameters is assessed. Finally, a virtual biodiversity experiment is conducted by testing the influence of varying the species richness and composition on ecosystem properties.

Abstract

Forest dynamic models predict the current and future states of ecosystems and are a nexus between physiological processes and empirical data, forest plot inventories and remote-sensing information. The problem of biodiversity representation in these models has long been an impediment to a detailed understanding of ecosystem processes. This challenge is amplified for species- and carbon-rich tropical forests. Here we describe an individual-based and spatially-explicit forest growth simulator, TROLL, that integrates recent advances in plant physiology. Processes are linked to species-specific functional traits in a parameterization for an Amazonian tropical rainforest. We simulate forest regeneration from bare soil, and validate it against observations at our sites. The simulated regeneration dynamics was comparable with observations for stem densities, productivity (GPP), aboveground biomass (AGB) and floristic composition. After 500 years of regrowth, the simulated forest presented structural characteristics similar to observations (e.g. leaf area index and tree diameter distribution). We then assessed model sensitivity to a number of key global parameters. Light extinction coefficient and carbon quantum yield, but also basal mortality rate and carbon allocation strongly influenced ecosystem features. Finally, we conducted a virtual biodiversity experiment by testing the influence of varying the species richness and composition on ecosystem properties. Species richness had overall a positive effect on ecosystem processes, but these were mostly controlled by species identity and functional trait community means, rather than richness per se and functional diversity. This suggests that site-specific species traits should be used to simulate ecosystem functioning. TROLL data requirement parallels current trait collection efforts, and this model should be applicable for many tropical forests sites. Model outputs are similar to field inventories. We believe this kind of approach can have a valuable contribution to increase the dialogue between the vegetation modeling community and ecology, to enhance model's predictive ability, and to inform policy choices.

Keywords: individual-based model, functional traits, tropical forest, productivity, biomass, biodiversity, Amazonia, spatially explicit, regeneration, plant community dynamics, vegetation dynamics, sensitivity analysis

Introduction

Much of the uncertainty in the current and future status of the carbon cycle is associated to the dynamics of terrestrial vegetation and its response to climate (Fisher et al., 2014). Tropical forests play a fundamental role in regional and global biogeochemical cycles (Malhi et al. 2008, Saatchi et al. 2011, Harper et al. 2013), and host over half of the Earth's biodiversity (Scheffers et al. 2012), and this amplifies the challenge of this research program. Dynamic vegetation models (DVMs) have been implemented to represent the role of vegetation in Earth system models (Prentice et al. 2007). However the development of robust DVMs at global scale is still facing major challenges. DVMs operate over large spatial grids (of typically 1° x 1° resolution) and they use a big-leaf approach to describe the balance in carbon, water and energy. In addition, the diversity in terrestrial vegetation is aggregated into less than a dozen plant functional types (PFTs), broadly defined by their geographical affinity, deciduousness and physiology (Sitch et al. 2003, Clark et al. 2011).

However, leaf and stem functional traits that govern plant physiology display a wide spectrum of variation within PFTs, and particularly so in species-rich tropical ecosystems (Fyllas et al. 2009, Baraloto et al. 2010, Díaz et al. 2016). By ignoring species diversity models may fail to describe features of vegetation structure or dynamics, such as productivity (Morin et al. 2011, Grace et al. 2016), biomass (Poorter et al. 2015) or stability (Loreau and de Mazancourt 2013, Morin et al. 2014). Better including functional diversity in DVMs should help increase their predictive power (Moorcroft 2006, Purves and Pacala 2008). New-generation models could even jointly model elemental cycles and the dynamics of biodiversity (Harfoot et al. 2014, Mokany et al. 2016, Van Bodegom et al. 2014).

Individual-based models of forest dynamics are a natural place to start when developing this approach. These models typically describe forest 'patches' as the unit of management (of typically 20 x 20 m), and these patches can either accumulate carbon through time, owing to the growth of trees within the patch, or release their carbon through gap opening, either artificial or natural (Bugmann 2001, Porté and Bartelink 2002). They have been primarily developed to inform forestry management both in temperate forests and in the tropics (Botkin et al. 1972, Shugart 1984, Vanclay 1991, Liu and Ashton 1995, Fischer et al. 2016). In these models, up to several dozens of different PFTs are typically defined, and some of them are fully spatially explicit (Pacala et al. 1996). Because they integrate finer-grained details of forest spatial heterogeneity and diversity than DVMs, these models have proved

useful in assimilating field data, representing forest stand growth dynamics and, ultimately, in deducing large-scale properties of ecosystems using a scaling-up approach (Moorcroft et al. 2001, Sato et al. 2007, Strigul et al. 2008, Fischer et al. 2016). However, these forest models have seldom been designed to explore vegetation responses to future changes in multiple interacting climate drivers since they mostly rely on empirical equations (Le Roux et al. 2001, Pretzsch et al. 2015). Also, it has been argued that individual based forest simulators models are of limited interest because they require too much computer power to be used at large scale (Strigul et al. 2008). With advances in plant physiology and in computer power, both limitations need to be critically reappraised (Shugart et al. 2015).

A number of steps have been taken to bridge the gap between DVMs and finer-grained models, so as to more efficiently assimilate information from emerging large plant trait databases (Kattge et al. 2011) and to account for demographic stochasticity (Strigul et al. 2008). Verheijen et al. (2013) allowed some traits to vary within PFTs in a DVM via trait-climate correlations drawn from large trait databases. Scheiter et al. (2013) and Fyllas et al. (2014) replaced PFTs by a trait continuum approach in modeled cohorts of individuals. Pavlick et al. (2013) and Sakschewski et al. (2015) constrained individual trait combinations by using documented plant economics spectra and plant strategies through simulations of forest models. These modeling approaches represent promising steps towards new-generation DVMs (Van Bodegom et al. 2012, 2014). However, these models take a 'taxonomy-free' extreme in the description of biological diversity, ignoring species-level differences and focusing on the continuum of traits. While this is a useful simplification, it is unclear how ecological processes, such as competition, facilitation, or multitrophic interactions, can be included in this approach. To illustrate this point, it has been abundantly documented that negative density-dependence is a major explanation for why tropical forest communities are hyperdiverse (Janzen 1970, Connell 1971, Wright 2002). Natural enemies, such as herbivores or pathogens, tend to negatively impact abundant species more than rare ones, a hypothesis which has been confirmed empirically (Harms et al. 2000, Bagchi et al. 2014, Comita et al. 2014). Yet trait-based approaches cannot easily account for such processes, and more generally it is important to explore the extent to which species richness may play an important role in understanding the functioning of forest ecosystems (Tobner et al. 2013, Sapijanskas et al. 2014, Toïgo et al. 2015).

A major question is whether forests with many species tend to have higher biomass, higher productivity, and more resilience to disturbances than those with a few species. Evidence for a relationship has been found in experimental setups (Hooper et al. 2005,

Scherer-Lorenzen et al. 2007), in natural vegetation (Vilà et al. 2007), and theoretical frameworks have been developed to understand the mechanisms underpinning predicted relationships (Loreau and Hector 2001, Hooper et al. 2005). If an ecosystem variable Y depends significantly on species richness S, this may be due to the increased likelihood of selecting high-performance species in species-rich communities compared with species-poor ones (the so-called selection effect), or to a synergistic effect of many-species communities (the so-called complementary effect, Loreau and Hector 2001). Individual-based forest simulators are appropriate to test these hypotheses (Morin et al. 2011, Forrester 2014), but this has never been done for tropical forests.

In this contribution, we integrate recent advances in plant physiological community processes modeling in the forest growth simulator TROLL, an individual-based and spatially-explicit forest model, and we relate these processes to species-specific functional traits in a parameterization for a tropical rainforest. More specifically, we (1) simulate the regeneration of a tropical rainforest from bare soil, and validate it against a range of observations at our sites; (2) assess model sensitivity to a number of key global parameters, and to the inclusion of negative density-dependence processes; (3) finally, we conduct a virtual biodiversity experiment by testing the influence of varying the species composition on ecosystem properties. These results shed light on the potential contribution of a model such as TROLL into the active research issue of improving predictive next-generation DVMs.

Model description

Overview

TROLL belongs to the family of individual-based and spatially explicit forest growth simulators, along with SORTIE (Pacala et al. 1996, Uriarte et al. 2009) and FORMIND (Köhler and Huth 1998, Fischer et al. 2016). It simulates the life cycle of individual trees (they recruit, grow, produce seeds and die) from a diameter size above 1 cm. Tree growth takes place in a forest light environment that is computed explicitly as a voxel space at metric scale. Each tree is defined by a set of biometric state variables (dbh, height, crown radius and crown depth, leaf area) and its age (Fig. 1). Tree geometry is set by allometric equations, but

leaf area varies dynamically within each crown (dependent on allocation). A single tree can establish per 1x1 m pixel. In contrast with previous forest simulators, tree growth is simulated from an explicit carbon balance calculation (assimilation plus allocation), with assimilation computed over half-hourly periods of a representative day, which in turn influences the environment at the next timestep, which is taken to be of one month. Seedlings below the 1-cm size class are not modeled explicitly, but are part of a seed/seedling pool. In this version of TROLL, belowground processes are not explicitly represented, and herbaceous plants (including epiphytes) and lianas are not included.

A species label is attached to each tree and is inherited from the mother tree through the seed. To this species label is associated a number of species-specific parameters (Table 1) corresponding to trait values that can be directly obtained from field measurements (see below).

The source code is written in C++ and is available upon request. Visualization, statistical analysis and data processing were performed in R version 3.0.2 (R Core Team 2013).
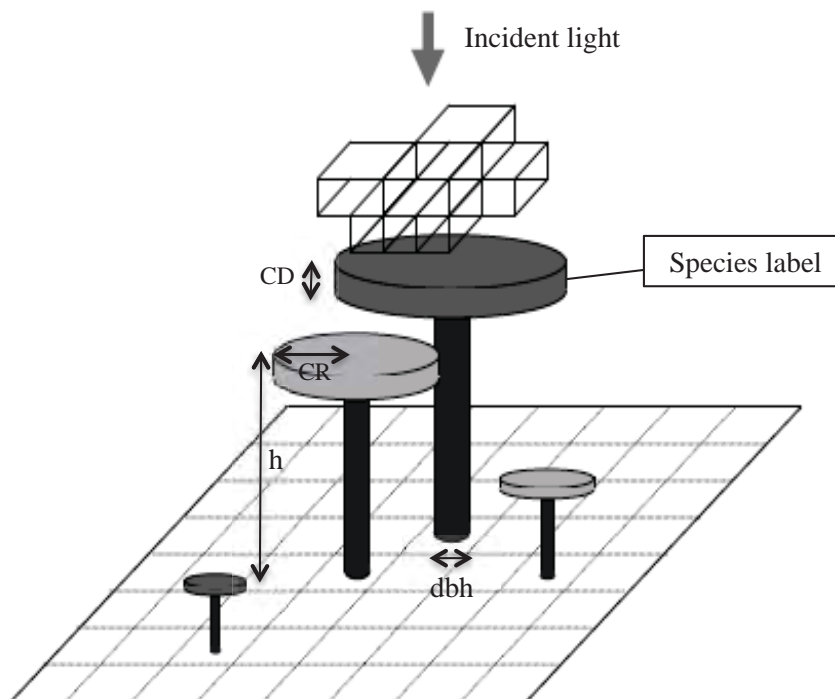
Fig. 1. Representation of individual trees in an explicit spatial grid in TROLL. Each tree is composed of a trunk and a crown, with cylinder shapes. The crown and trunk dimensions (crown radius, CR; crown depth, CD; height, h; diameter at breast height, dbh) are updated at each timestep, depending on the assimilated carbon that is allocated to growth, and following allometric relationships. To each tree is associated a species label with species-specific parameters (see Table 1). Light diffusion is computed explicitly at each timestep and within each voxel from top canopy to the ground.

Table 1. Species-specific parameters provided in input of the TROLL model. All data are from the BRIDGE (Baraloto et al. 2010) and TRY (Kattge et al. 2011) datasets, except some species values of LMA, N and P (Maréchaux & Chave, unpublished data).

Abbreviation	Description	Units
LMA	leaf mass per area	g/m^2
N	leaf nitrogen content per dry mass	mg/g
P	leaf phosphorous content per dry mass	mg/g
wsg	wood specific gravity	g/cm^3
dbh$_{max}$	maximal diameter at breast height	m
h$_{lim}$	asymptotic height	m
a$_h$	parameter of the tree-height-dbh allometry	m

Modeling the abiotic environment

Within-canopy heterogeneity is explicitly modeled at metric scale. The physical space in which trees grow is described as a three-dimensional grid discretized into voxels 1x1x1 m (i.e. 1 m^3, Fig. 1). The maximal tree size (up to 60-80 m), serves as an upper threshold for the upward extension of the voxel space.

For each tree crown, leaf area density is deduced from tree geometry assuming that a tree distributes its leaf area uniformly across the voxels its crown occupies (voxel-mean leaf density LD, in m^2/m^3). Cumulating over all the trees, a leaf area density (leaf area per voxel; in m^2/m^3) is computed within each simulated voxel v, denoted $LAD(v)$. The vertical sum of LAD, upwards from each voxel, defines

$$LAI(v) = \sum_{v'=v}^{\infty} LAD(v') \tag{1}$$

$LAI(v)$ for ground-layer voxels v, commonly called LAI (leaf area index), is the cumulative leaf area density down to the ground level (leaf area per ground area, in m^2/m^2), and is a common metric in forestry. It ranges between 5 and 7 in closed tropical canopy-forests (Clark et al. 2008). Terrestrial lidar scanning technology allows a direct measurement of LAD(v) in forests (Calders et al. 2015).

To compute carbon assimilation, we prescribe the daily course of variation in light intensity (PPFD, in µmol photons m^{-2}s^{-1}), temperature (T, in degrees Celsius), and the vapor pressure deficit (VPD, in kPa) within each voxel of the canopy and for a representative day

per month (Appendix 1). To this end, we model the within canopy variation in PPFD as a local Beer-Lambert extinction law:

$$PPFD_{max,month}(v) = PPFD_{top,max,month} \times \exp[- k \times LAI(v)] \tag{2}$$

where the monthly average of the daily maximum incident photosynthetic PPFD at top canopy (PPFD$_{top,max,month}$) is prescribed from measurements. We assume a uniform extinction rate k (values for each parameter are reported in Table 2). The extinction rate k is expected to vary with zenith angle and species leaf inclination angle (Meir et al. 2000, Kitajima et al. 2005). Considering the importance of light limitation in the understory of tropical forests, we expect the model to be sensitive to the choice of k. In this version of the model, we considered only vertical light diffusion, ignoring more complex light models within vegetation canopies (Canham et al. 1994, Brunner 1998) or even full radiative transfer models (Gastellu-Etchegorry et al. 1996, Lewis 1999, Mercado et al. 2009a, Widlowski et al. 2013). Temperature and VPD also decrease with forest canopy depth and during half-hourly time steps t of a representative day per month, resulting in light intensity $PPFD_{month}(v,t)$, temperature $T_{month}(v,t)$ and $VPD_{month}(v,t)$ (Appendix 1).

Table 2. Global parameters used in TROLL. When specified, values in brackets correspond to the distribution range used for the sensitivity analysis.

Abbreviation	Description	Units	Values	Source
k	light extinction coefficient, used in light diffusion Beer-Lambert law	-	0.90 [0.50;0.95]	Wirth et al. 2001, Cournac et al. 2002
ϕ	apparent quantum yield for C fixation	mol$C$/mol *photons*	0.06 [0.04;0.09]	Domingues et al. 2014, L. Verryckt unpublished data
g_1	stomatal conductance parameter	kPa$^{1/2}$	3.77 [2;5]	Lin et al. 2015
f_{wood}	fraction of NPP allocated to wood growth	-	0.35 [0.20;0.45]	Aragão et al. 2009, Malhi et al. 2011
f_{canopy}	fraction of NPP allocated to canopy, including leaves*, fruits and twigs	-	0.30 [0.20;0.45]	Aragão et al. 2009, Malhi et al. 2011
m	maximal basal mortality rate	-	0.02 [0.01;0.05]	

* The fraction of NPP allocated to leaves only is set at 0.68$\times$ f$_{canopy}$ according to Chave et al. (2008, 2010)

In the future, coupling with a full energy transfer model could replace these equations. Alternatively, the model could input empirical half-hourly datasets of PPFD, T and VPD. In its current version, TROLL does not explicitly calculate the water balance in the soil and the soil-plant-atmosphere water column (Williams et al. 1996, Granier et al. 1999, Laio et al.

2001), and it also ignores the dynamics of nutrients in the soil (Goll et al. 2012), and assumes fixed species-specific leaf nutrient concentrations. These additions are left to subsequent contributions.

Photosynthetic carbon uptake by plants: leaf-level theory

The first version of TROLL assumed an empirical form of the growth of tree trunk diameters, as in most forest gap models (Chave 1999). Here, we include a description of the carbon uptake for each plant, with the Farquhar, von Caemmerer and Berry model of C_3 photosynthesis (Farquhar et al. 1980). Gross carbon assimilation rate (A, $\mu molCO_2$ $m^{-2}s^{-1}$) is limited by either Rubisco activity (A_v), or RuBP regeneration (A_j) as follows:

$$A = \min\{A_v, A_j\} \qquad A_v = V_{cmax} \times \frac{c_i - \Gamma^*}{c_i + K_m} \qquad A_j = \frac{J}{4} \frac{c_i - \Gamma^*}{c_i + 2\Gamma^*} \qquad (3)$$

where V_{cmax} is the maximum rate of carboxylation ($\mu molCO_2$ $m^{-2}s^{-1}$), c_i the CO_2 partial pressure at carboxylation site, Γ^* the CO_2 compensation point in the absence of dark respiration, K_m the apparent kinetic constant of the Rubisco (von Caemmerer 2000), and J the electron transport rate ($\mu mol e^-$ $m^{-2}s^{-1}$). In this model, J itself depends on PPFD through

$$J = \frac{1}{2\theta} \left[\alpha \times PPFD + J_{max} - \sqrt{(\alpha \times PPFD + J_{max})^2 - 4\theta \times \alpha \times PPFD \times J_{max}} \right] \qquad (4)$$

where J_{max} is the maximal electron transport capacity ($\mu mol e^-$ $m^{-2}s^{-1}$), θ the curvature factor, and α the apparent quantum yield to electron transport (mole^-/mol *photons*). In the following we use ϕ, the apparent quantum yield for C fixation (mol$C$/mol *photons*), which is empirically measured as the initial slope of the photosynthetic assimilation plotted against incident irradiance. Note that four electrons are needed to regenerate RuBP, so $\alpha = 4\phi$. In this photosynthesis model, ϕ, V_{cmax} and J_{max}, are key parameters, and uncertainty in these parameters represents a large source of uncertainty in vegetation models (Zaehle et al. 2005, Mercado et al. 2009b, Rogers 2013).

Carbon assimilation by photosynthesis is limited by the CO_2 partial pressure at carboxylation site, which is controlled by stomatal transport as modeled by the diffusion equation:

$$A = g_s(c_a - c_i) \qquad (5)$$

with g_s the stomatal conductance to CO_2 (molCO_2 $m^{-2}s^{-1}$). In most DVMs, leaf stomatal conductance is modeled empirically as a function of the VPD (Ball et al. 1987, Leuning 1995). We instead used the model developed by Medlyn et al. (2011):

$$g_s = g_0 + \left(1 + \frac{g_1}{\sqrt{VPD}}\right)\frac{A}{c_a} \tag{6}$$

where g_0 and g_1 are parameters. Medlyn et al. (2011)'s model results from an optimization argument, according to which stomata should act to maximize carbon gain while minimizing water loss (Cowan and Farquhar 1977). Assuming $g_0 \approx 0$, an empirically reasonable assumption, and coupling (5) and (6), this leads to:

$$\frac{c_i}{c_a} = \frac{g_1}{g_1 + \sqrt{VPD}} \tag{7}$$

so the c_i/c_a ratio declines as VPD increases. Focusing on the light-limited part of the Farquhar model, this shows that $g_1 \propto \sqrt{\Gamma^*}$ which suggests that g_1 increases with temperature. Using a different optimal theory pathway and focusing on the Rubisco-limited part of the Farquhar model, Prentice et al. (2014) derived the same expression as equation (7), but with $g_1 \propto \sqrt{K_m}$, also suggesting a strong dependence of g_1 on temperature.

Photosynthetic carbon uptake by plants: leaf-level parameterization

Photosynthetic efficiency depends on leaf nutrient content and other leaf traits (Reich et al. 1997, Wright et al. 2004). In tropical forest environments, Domingues et al. (2010) found that V_{cmax} and J_{max} are co-limited by the leaf concentration of nitrogen (N) and phosphorus (P):

$$\log_{10} V_{cmax-M} = min \begin{cases} -1.56 + 0.43 \times \log_{10} N - 0.37 \times \log_{10} LMA \; ; \\ -0.80 + 0.45 \times \log_{10} P - 0.25 \times \log_{10} LMA \end{cases} \tag{8}$$

$$\log_{10} J_{max-M} = min \begin{cases} -1.50 + 0.41 \times \log_{10} N - 0.45 \times \log_{10} LMA \; ; \\ -0.74 + 0.44 \times \log_{10} P - 0.32 \times \log_{10} LMA \end{cases} \tag{9}$$

with V_{cmax-M} and J_{max-M} the photosynthetic capacities at 25°C of mature leaves on a leaf dry mass basis, in $\mu mol CO_2 \, g^{-1} s^{-1}$ and $\mu mol e^- \, g^{-1} s^{-1}$, respectively. N and P are the leaf nitrogen and phosphorous contents in mg/g, and LMA is the leaf mass per area in g/cm^2. V_{cmax-M} and J_{max-M} can be converted into area-based V_{cmax} and J_{max} by multiplying by LMA. Recent modeling studies on Amazonian forests have implemented this model for Amazonian forests (Mercado et al. 2011, Fyllas et al. 2014). To account for variation of V_{cmax} and J_{max} with temperature, we used the formulas of Bernacchi et al. (2003) and enzymatic kinetic constant values and their temperature relationships as published in von Caemmerer (2000, Domingues et al. 2010; see Appendix 2). Long-term acclimation to temperature is not included here as simulations were conducted in a stable climate, and is left for future developments (Kattge and Knorr 2007, Smith and Dukes 2013).

The stomatal conductance model (eqs. 5-6) depends on g_1, which is expected to vary with whole-plant water-use efficiency, or marginal carbon cost of water use. It has indeed been found to vary among plant functional types (Lin et al. 2015a). Given the lack of direct measurements of g_1 at species level and of a robust relationship with other functional traits, we here used a fixed mean value of g_1 (Table 2). We expect a high sensitivity of the stomatal conductance model to the value of the g_1 parameter (Knauer et al. 2015, Kala et al. 2015, 2016).

Leaf carbon assimilation A_l is finally computed for each tree and within each crown layer l (in $\mu mol CO_2$ m^{-2}s^{-1}), as follows:

$$A_l = \frac{1}{n_v \times t_M} \times \sum_v \sum_{t=1}^{t_M} A(PPFD_{month}(v,t), VPD_{month}(v,t), T_{month}(v,t)) \tag{10}$$

where the microclimatic variables are taken from Appendix 1 and A_l averaged across the n_v voxels within crown layer l, and over the half-hourly intervals of a typical day (where t_M represents the number of half-hourly values of daytime).

Autotrophic respiration

Plants metabolize a large fraction of their carbon uptake for maintenance and growth, and this autotrophic respiration contributes typically 30-65% of the gross primary productivity (Malhi 2012). It varies strongly among species, within and across sites (Slot et al. 2013, Atkin et al. 2015) and due to the environment (Atkin et al. 2005, Wright et al. 2006). However, this process constitutes a major source of uncertainty in the modeling carbon fluxes (Huntingford et al. 2013, Atkin et al. 2014). We partitioned autotrophic respiration into maintenance respiration and growth respiration, acknowledging that they come from the same biochemical pathways (Amthor 1984, Thornley and Cannell 2000).

Maintenance respiration ($R_{maintenance}$) is usually inferred empirically (Meir et al. 2001, Cavaleri et al. 2008, Slot et al. 2013, Weerasinghe et al. 2014), and has seldom been documented for stem and roots. Atkin et al. (2015) compiled a database of mature leaf dark respiration and associated leaf traits for 899 species of 100 sites worldwide, spanning a wide range of biomes including tropical forests. We used their broadleaved trees model for leaf maintenance respiration:

$$R_{leaf-M} = 8.5341 - 0.1306 \times N - 0.5670 \times P$$
$$-0.0137 \times LMA + 11.1 \times V_{cmax-M} + 0.1876 \times N \times P \tag{11}$$

with $R_{\text{leaf-M}}$ the leaf dark respiration rate on a dry mass basis and at reference temperature of 25°C, in $\text{nmol}CO_2$ $\text{g}^{-1}\text{s}^{-1}$. The other terms are as in Equation (8-9). Multiplying $R_{\text{leaf-M}}$ by LMA gives an area-based R_{leaf} (in μmolC $\text{m}^{-2}\text{s}^{-1}$). For consistency, we used the same temperature dependencies for leaf respiration as in Atkin et al. (2015; see also Heskel et al. 2016). We assumed leaf respiration rate during day light to be 40% of leaf respiration in the dark at the typical range of temperatures at our site (Atkin et al. 2000). Total leaf respiration per timestep is then calculated by explicitly accounting for the length of daylight.

Stem maintenance respiration (R_{stem}, in μmolC/s) is modeled assuming a constant respiration rate per volume of sapwood (Ryan et al. 1994), so that:

$$R_{stem} = 39.6 \times \pi \times ST \times (dbh - ST) \times (h - CD) \tag{12}$$

with dbh, h, CD, ST tree diameter at breast height, total tree height, crown depth, and sapwood thickness respectively (all in m). We assumed that ST= 0.04 m for trees with a dbh>30cm and that ST increases with dbh from 0 to 0.04 m for smaller trees in agreement with empirical studies (Granier et al. 1996, Meir and Grace 2002). Stem respiration response to temperature was modeled using a Q_{10} value of 2.0 (Ryan et al. 1994, Meir and Grace 2002). Stahl et al. (2011) reported that R_{stem} varies among individual trees, even when controlling for sapwood volume. However, in the absence of a more precise understanding of the causes of variation, we used Equation (12). Also, Stahl et al. (2010) and van der Sande et al. (2015) showed that ST can vary significantly across conspecific trees and among species, but the model assumed here is a reasonable first step.

Fine root maintenance respiration was assumed to be half of leaf maintenance respiration (Malhi 2012), and coarse root and branch maintenance respirations were assumed to account for half of stem respiration (Meir and Grace 2002, Cavaleri et al. 2006, Asao et al. 2015). Finally, growth respiration (R_{growth}) was assumed to account for 25% of the carbon uptake by photosynthesis (gross primary productivity) minus the maintenance respiration (Cannell and Thornley 2000). These assumptions are commonly made in the literature, but in the future, it would be desirable to provide more precise models.

Net carbon uptake: whole-tree integration and allocation

At each timestep, individual net primary production of carbon NPP_{ind} (in gC) is obtained by the following balance equation:

$$NPP_{ind} = GPP_{ind} - R_{maintenance} - R_{growth} \tag{13}$$

To calculate NPP_{ind}, area-based NPP must be summed over the crown's leaf area. Leaf area is partitioned into three pools corresponding to the following leaf age classes: young, mature and old leaves, so that LA= LA$_{young}$ + LA$_{mature}$ + LA$_{old}$ (all in m^2). Young leaves and old leaves have lower photosynthetic capacities and activities than mature leaves (Kitajima et al. 1997, 2002, Doughty and Goulden 2008, De Weirdt et al. 2012, Wu et al. 2016). We assumed that young and mature leaves have assimilation and respiration rates half that of mature leaves (see eqs. 3 and 11), so that:

$$GPP_{ind} = 189.3 \, \Delta t \times \sum_{l=\lfloor h-CD \rfloor+1}^{\lfloor h \rfloor} [A_l] \times (0.5 \times LA_{young} + LA_{mature} + 0.5 \times LA_{old}) \quad (14)$$

where h is tree height, CD tree crown depth and $\lfloor x \rfloor$ is the rounding function, Δt the duration of a timestep (in yr). The factor 189.3 converts a rate from $\mu mol CO_2$ m^{-2}s^{-1} into gC m^{-2} year^{-1} (with 12 the molar mass of C, an average number of days per year of 365.25 and assuming 12 hours of assimilation per day throughout the year). At each timestep, respiration terms are also converted into gC.

Carbon allocation to plant organs is prescribed by fixed factors derived from empirical studies at our sites (Chave et al. 2008b) or elsewhere in Amazonia (Aragão et al. 2009, Malhi et al. 2011, 2015). Carbon allocated to wood is converted into an increment of stem volume, ΔV in m^3, as follows:

$$\Delta V = 10^{-6} \times \frac{f_{wood} \times NPP_{ind}}{0.5 \times wsg} \times Senesc(dbh) \quad (15)$$

where f_{wood} is the fixed fraction of NPP allocated to aboveground woody growth (i.e., stem and branches), wsg is the species-specific wood specific gravity (g/cm^3; Table 1) and the factor 0.5 converts dry biomass units into carbon units (Elias and Potvin 2003, Thomas and Martin 2012). We assumed that large trees 'senesce', i.e. they cannot convert NPP as efficiently into growth, reflecting empirical evidence of a size-related growth decline in trees (Yoda et al. 1965, Ryan et al. 1997, Woodruff and Meinzer 2011). When the tree dbh is lower than a species-specific threshold dbh$_{max}$ (Table 1), then $Senesc(dbh) = 1$. If it is larger, then $Senesc(dbh) = \max\left(0; 3 - 2\frac{dbh}{dbh_{max}}\right)$. So trees are assumed to be in the senescent phase if $dbh_{max} \leq dbh \leq \frac{3}{2} dbh_{max}$, and they cannot further grow beyond $dbh = \frac{3}{2} dbh_{max}$.

Next the fraction of NPP allocated to the tree canopy is denoted f$_{canopy}$, further decomposed into leaf, twig and fruit production i.e. f$_{canopy}$= f$_{leaves}$+ f$_{fruit}$+ f$_{twigs}$. Carbon allocated to leaf production results in a new young leaf pool, and leaf area dynamics obey the following equations:

$$\Delta LA_{young} = \frac{2 \times f_{leaves} \times NPP_{ind}}{LMA} - \frac{LA_{young}}{\tau_{young}}$$

$$\Delta LA_{mature} = \frac{LA_{young}}{\tau_{young}} - \frac{LA_{mature}}{\tau_{mature}}$$

$$\Delta LA_{old} = \frac{LA_{mature}}{\tau_{mature}} - \frac{LA_{old}}{\tau_{old}} \tag{16}$$

where τ_{young}, τ_{mature}, τ_{old} are species-specific residence times in each class (in yr), LL is the species-specific leaf lifespan (in yr), so that LL= τ_{young}+τ_{mature}+τ_{old}. In this model, we infer LL from LMA for each species, using the equation proposed by Reich et al. (1991), τ_{young} was fixed to 1/12 yr for all species (one month; Doughty and Goulden 2008, Wu et al. 2016), and τ_{mature} as a third of the leaf lifespan. The loss term LA_{old}/τ_{old} corresponds to the rate of leaf litterfall at each timestep. Thus, litterfall results from the dynamics of leaf biomass and specific leaf life spans. This is unlike Wu et al. (2016) where litterfall was prescribed, Forrester and Tang (2016) where litterfall was a constant fraction of leaf stock, or De Weirdt et al. (2012) where it was assumed equal to the biomass allocated to leaves (implying a constant total leaf area). Belowground carbon allocation was not included explicitly in this version of the model. As the allocation factors f_{wood} and f_{canopy} drive the pathway from tree productivity to aboveground biomass (AGB) and structure, we expect a high model sensibility to these parameters.

Tree growth and allometries

Trunk diameter growth in dbh, Δdbh, is computed from ΔV (eq. 15), as follows. We assumed that tree height is inferred from the dbh value using a Michaelis-Menten equation:

$$h = h_{lim} \frac{dbh}{dbh+a_h} \tag{17}$$

with h_{lim} and a_h, species-specific parameters derived from local measurements on standing trees (Baraloto et al. 2010, Table 1). Note that since $dbh \leq \frac{3}{2} dbh_{max}$, h is bounded upwards by a value lower than h_{lim}, which we call $h_{max} = h_{lim} \frac{3dbh_{max}}{3dbh_{max}+2a_h}$. Since $V = C\,\pi(\frac{dbh}{2})^2 h$, then:

$$\Delta V = C \frac{1}{2}\pi h \times dbh \times \Delta dbh + C\,\pi(\frac{dbh}{2})^2 \Delta h = V \frac{\Delta dbh}{dbh}\left(3 - \frac{dbh}{dbh+a_h}\right) \tag{18}$$

or, equivalently, $\frac{\Delta V}{V} = \frac{\Delta dbh}{dbh}\left(3 - \frac{h}{h_{lim}}\right)$. Here, C is a form factor (Chave et al. 2014, eq. 5 therein). Hence, Δdbh can be deduced from ΔV directly from equation (18) above.

Tree crown dimensions are also updated using allometric equations. We used a single allometric relationship between crown radius and dbh, and between crown depth and tree height, as follows:

$$CR = 0.80 + 10.47{\times}dbh - 3.33{\times}dbh^2 \qquad (19)$$

$$CD = -0.48 + 0.26{\times}h \; ; \quad CD = 0.13 + 0.17{\times}h \; (h < 5\,m) \qquad (20)$$

Equations (19) and (20) are based on 168 measurements carried out in French Guiana (Chave et al. 2005; with RMSE=0.67 m, R^2=0.74, P<10^{-15} and RMSE=2.63 m, R^2=0.38, P<10^{-15} for eqs. 19 and 20 respectively). Since we lacked species-specific information, we used the same relationships linking crown radius to dbh and crown depth to tree height across all species. For equations (17), (19) and (20), patterns of variation in trees have motivated a great deal of literature (Feldpausch et al. 2011, Lines et al. 2012, Chave et al. 2014). Tree crown architecture depends on ecological strategies (Bohlman and O'Brien 2006, Poorter et al. 2006, Iida et al. 2012). A future version of the model could integrate species-specific allometries for crown dimensions and improved relations for total tree height.

Finally, the mean leaf density within the crown (*LD,* in m^2/m^3) is computed as:

$$LD = \frac{LA_{young} + LA_{mature} + LA_{old}}{\pi{\times}CR^2{\times}CD} \qquad (21)$$

It depends on crown volume and total leaf density, assuming a uniform distribution of leaf area within the crown.

Mortality

Mortality processes are complex and still incompletely represented in current vegetation models, although they play a key role in forest structure and carbon balance (Delbart et al. 2010, Sevanto et al. 2014, Johnson et al. 2016). At each timestep, each tree simulated in TROLL has a probability *d* to die, computed as follows:

$$d = d_b + d_t + d_{NDD} \qquad (22)$$

where d_b is a background death rate, d_t represents death due to treefalls, and d_{NDD} represents death due to negative density dependence.

Background mortality d_b varies greatly among species, and we here assume that it is negatively correlated with wood density, as observed pan-tropically (King et al. 2006, Poorter et al. 2008, Wright et al. 2010, Kraft et al. 2010). This dependence illustrates a trade-off between investment into construction costs and risk of mortality (Chave et al., 2009). More precisely, we assumed the simple following relationship:

$$d_b = m \times \left(1 - \frac{wsg}{wsg_{lim}}\right) + d_n \tag{23}$$

where m (in events/yr) is the reference background mortality rate for a species with very low wood density, typically a pioneer species. It was tuned to fit observation of overall stem mortality rates. wsg_{lim} is a value large enough so that d_b always remains positive (here set at 1). The parameter d_n represents death caused by carbohydrate shortage in case of prolonged stress. For each stem, we record the duration during which the tree is under a negative carbon balance, defined as $NPP_{ind} < 0$ (eq. 13). When the stress duration exceeds the tree leaf lifespan, d_n is set to 1 and the tree dies of carbon starvation, d_n equals 0 otherwise.

Tree death may also be caused by treefalls at a rate d_t. To simulate this process, we first define a stochastic threshold Θ computed for each tree depending on species-specific structural features as follows:

$$\Theta = h_{max} \times (1 - v_T \times |\zeta|) \tag{24}$$

where h_{max} is the maximal tree height, v_T is a variance term (here set at 0.3), $|\zeta|$ is the absolute value of a random Gaussian variable with zero mean and unit standard deviation. If the tree height exceeds Θ, then the tree falls with a probability equal to $1 - \Theta/h$ (Chave 1999). The treefall direction is drawn uniformly in $[0, 2\pi]$. Trees on the trajectory of the falling tree can be damaged, especially if they are smaller than the fallen tree (van der Meer and Bongers 1996). An individual variable *hurt* is incremented by h and $\frac{h-CR}{2}$ respectively (h and CR being the tree height and crown radius of the fallen tree) for the trees impacted by the falling. If a tree height is lower than its *hurt* value, it death probability is $1 - \frac{1}{2}\frac{h}{hurt}$. Each *hurt* variable is reset to zero at each timestep.

Finally, we simulated mortality caused by biotic negative-density dependent effect (term d_{NDD}). The fitness of abundant species is reduced because they tend to attract more their specific predators or pathogens (Wright 2002, Gonzalez et al. 2010, Zhu et al. 2015). Density-dependence is strongest between conspecific individuals (Gonzalez et al. 2010, Comita et al. 2010, Paine et al. 2012). Here, we hypothesize that basal area is a good proxy for modeling negative density dependence and that this effect is identical across species. At each site i and species s, we computed the term:

$$NDD_{i,s} = \frac{1}{\pi R^2 BA} \sum_{\substack{j \\ trees\ of\ species\ s \\ with\ d_{i,j} < R}} BA_j \tag{25}$$

where BA_j is the basal area of a conspecific neighboring tree j, BA is the mean basal area of the stand (m²/ha), and R is the radius of the neighborhood, set to 15m (Uriarte et al. 2004, Comita and Hubbell 2009, Zhu et al. 2015). From equation (25) we compute d_{NDD} as follows:

$$d_{NDD} = \Delta_d \times NDD_{i,s} \left(1 - 2\frac{dbh}{dbh_{max}} \right) \tag{26}$$

where Δ_d determines the strength of NDD on mortality. Here, we assume that d_{NDD} decreases linearly with the size of the focal tree (Uriarte et al. 2004, Zhu et al. 2015) and equals 0 when it reaches a size of $dbh_{max}/2$.

Seed production, dispersal and recruitment

We assumed trees become fertile above a given height threshold that is species-specific (h_{mature} ; Wright et al., 2005), computed from h_{max} as follows:

$$h_{mature} = -11.47 + 0.90 \times h_{max} \tag{27}$$

This relationship is drawn from data of reproductive status of 11 species at Barro Colorado Island, Panama (Wright et al. 2005) and 11 species from Pasoh Forest Reserve, West Malaysia (Thomas 1996), all with h_{max}>20m (see Figure 5 in Wright et al., 2005; R^2=0.67, p=3,2.10[-6], n= 22 species). In the following, a seed may be interpreted as an opportunity of seedling recruitment rather than as a true seed, since not every single seed production and dispersion is modeled and the seed-to-seedling transition is implicit.

At each timestep, each mature tree has a probability of producing seeds. The number of reproduction opportunities per timestep and per mature tree (n_s) is assumed fixed and equal for all species (here set at 10). This assumption is predicated on the fact that there is a trade-off between seed number and survival and recruitment probability (which is related to seed size). Thus the probability of germination does not depend strongly on seed size or number of produced seeds and can be assumed a zero-sum game (Coomes and Grubb 2003, Moles et al. 2004, Moles and Westoby 2006). Note that irregular seed production, such as mast fruiting, is known to be frequent reproductive strategies in tropical woody species (Norden et al. 2007), but this is not considered in this version of the model.

Each of these n_s events is scattered away from the tree at a distance randomly drawn from a Gaussian distribution. In addition, we consider n_{ext} events due to seeds immigrating from the outside. These are calculated as follows:

$$n_{ext} = N_{tot} \times f_{reg} \times n_{ha} \tag{28}$$

where N_{tot} is the total number of reproduction opportunities per hectare coming from outside, f_{reg} the species regional frequency and n_{ha} the number of hectares of the simulated plot. These reproduction opportunities are uniformly distributed within the plots.

On each grid point of the ground, a 'seed' bank is defined, which is fed by the dispersal events from all the species. A recruitment event takes place if ground-level light availability is sufficient, i.e. above a species-specific light compensation point (LCP, which is set equal to R_{leaf}/ϕ). If several species are competing for recruitment, competition occurs and one of the species is picked at random as the winner out of the available species, as in a classic lottery model (Chesson and Warner 1981). A negative density dependence was also implemented at seedling recruitment stage. For seed/seedlings in the bank, and for each empty site i, we defined $p_{i,s}$ the probability of species s to establish, given that a seed of species s is present. This probability decreases with $NDD_{i,s}$ as follows:

$$p_{i,s} \propto \frac{1}{1+\Delta_r \times NDD_{i,s}} \tag{29}$$

where Δ_r is a parameter which determines the strength of negative density-dependence at the recruitment stage. If $\Delta_r = 0$ this model is equivalent to the lottery model.

Each newly recruited tree has initial size variable values, which we assume to be identical across species (dbh=0.01m, h=1m, CR=0.5m, CD=0.3m, LD=0.8 m^2/m^3).

Parameterization, validation data, and tests

Study sites and calibration/validation data

The TROLL simulator was parameterized for an Amazonian forest of French Guiana. Forests of the Guiana Shield cover some 30% of Amazonia (c.a. 1.6 million km^2), grow on Precambrian crystalline substrates (Quesada et al. 2010) and are known to have a distinct species composition (ter Steege et al. 2006), a high biomass and a low mortality rate (Johnson et al. 2016), and a tall canopy (Feldpausch et al. 2011) compared with western Amazonian forests. The study area receives c.a. 3000 mm/yr rainfall, with significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. A long wet season lasts from December to July, often interrupted by a short dry period in March. The dry season lasts from the end of August to November with 2-3 months with precipitation <100

mm/mo (Bongers et al. 2001). Air relative humidity is typically lower and temperature higher during the dry season due to low cloud coverage.

All input data were obtained from two research stations located in primary forest. The Nouragues Ecological Research Station is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05' N, 52°40' W; Bongers et al., 2001). The Paracou Research Station is located close to the village of Sinnamary and 20 km from the coast (5°15' N, 52°55' W; Gourlet-Fleury et al., 2004). Meteorological input data (PPFD, T and relative humidity, RH) were obtained from half-hourly measurements (Hukseflux SR11, Delft, Netherlands; Vaisala HMP155A, Vantaa, Finland), logged in an open area at the Nouragues Ecological Research Station from January to December 2014. Half-hourly VPD was deduced from relative humidity and temperature using known formulas (Monteith and Unsworth 2008). In this contribution, the same climate inputs were used every year throughout the simulations, resulting in a stable and periodic climate.

Species-specific parameters of TROLL were obtained for 163 species (Table 1). The allometric parameters were derived from ground data (Chave et al. 2005, Baraloto et al. 2010). Functional traits (LMA, wood density, leaf nutrient concentrations) were obtained from a trait database gathered in French Guiana (Baraloto et al. 2010). The species included in this study represent about 70% of the trees > 10cm dbh recorded in permanent plot censuses. Palms were excluded from the model simulations. Species regional frequencies used to parameterize the external seed rain (f_{reg}; eq. 29) were computed as species relative abundance in a 25-ha permanent plot (P16) at Paracou, and where all trees >10cm dbh within the plot were identified. All other general parameters were either measured at our sites or drawn from literature (see Table 2).

Model outputs were compared against tree density, basal area and aboveground biomass, of mature undisturbed forest plots. Specifically, we used data from a 25 ha plot located at the Paracou Station and 22 ha of plots at the Nouragues Station. In both plots, all trees ≥ 10cm were located, identified to the species, and measured at least every five years since the early 1990s (Chave et al. 2008b, Rutishauser et al. 2010). Empirical gross primary productivity for mature forest were provided by measurements from an eddy-flux tower located in the Paracou research station (Guyaflux; Bonal et al. 2008, Malhi 2012). Leaf fall was validated against measurements made from litterfall trap collection at both Paracou and Nouragues research stations (Chave et al. 2010).

Short-term outputs of the simulations were validated against tree inventory data of a 25-ha stand that was clearcut in 1976 and has been left regrowing since then. The site is

located South of the Sinnamary village, about 10 km west of the Paracou station (ARBOCEL plot; unpublished results). At this site, a 6.25-ha plot was set up by CIRAD in 1989 and it has been reinventoried every two years since then.

Simulating forest regeneration

We tested the TROLL model's ability to reproduce the successional dynamics of a tropical forest, including changes in its composition and structure. We simulated regeneration from bare soil within an area of 400x400 m, with a constant seed external input and during 500 yrs with monthly timesteps. The parameter set chosen for this simulation was taken from literature values (Table 2), with no fine-tuning of the parameter values.

It is assumed that after 500 yrs of regeneration, a forest should have reached maturity, in the absence of abiotic disturbances. Since we were interested in following the regeneration trajectory, no spin-up was performed. A typical simulation ran for about 90 min on a portable computer with a 1.7 GHz Intel processor.

In order to assess the variability of simulated forest properties due to stochasticity alone, we ran 100 replicates and computed the variance across runs.

Sensitivity analysis

To assess the sensitivity and overall goodness of fit of our model, we next performed a sensitivity analysis on a subset of the parameters. The analysis was conducted by replicating the simulation a thousand times with values of the six parameters drawn randomly and independently for each simulation from a prior distribution. Simulations were conducted on a 32-thread cluster (8-core Intel Xeon E5-2450 at 2.10 GHz).

We focused on the following six global model parameters (Table 2): light extinction coefficient (k), the apparent quantum yield (ϕ), stomatal conductance parameter g_1, NPP fraction allocated to wood growth (f_{wood}), NPP fraction allocated to canopy (f_{canopy}), and maximal mortality rate (m). These parameters were selected because we expected that they would be important for model outputs, and/or because few direct measurements are available, leading to uncertainties in their values. Each parameter was drawn in a uniform distribution, with ranges based on extreme values as reported in the literature (Table 2).

Model sensitivity was assessed both for the early stages of the regeneration dynamics and for the mature forest stage. For the beginning of the regeneration, we computed the root-mean-square error (RMSE) of the modeled aboveground biomass (AGB), number of trees $\geq$ 10 cm and $\geq$ 30 cm dbh against measured values from the regeneration plot (ARBOCEL plot), for the timesteps corresponding to its census dates (n=13). Variation of the RMSEs for these four outputs was plotted against each parameter values. For the mature forest stage, we computed the output averages over the 20 last timesteps of each simulation, and plotted these values against parameters values. We also investigated the covariation of these simulated output averages across the 1000 simulations, and their dependence on parameters values.

To quantify the sensitivity of the model to negative density-dependence as implemented in TROLL, we tested different intensities of negative density-dependence effect on mortality and recruitment (Δ_d, Δ_r, respectively). We tested a range of these parameter values, and fixed their ratio so that they have a similar effect on recruitment and mortality. In other words, we set the magnitude of density-dependence so that $\Delta_r = 100\alpha$; $\Delta_d = \alpha$, with $\alpha \geq 0$. We compared simulations against simulations with no effect ($\alpha = 0$). We compared simulated communities using the Inverse Simpson Diversity index (or effective number of species, Jost 2006). We tested the prediction that negative density-dependence increases biodiversity and investigated its influence on ecosystem processes. For all other simulations made in this study, we included no effect of negative density-dependence ($\alpha = 0$).

Role of biodiversity on ecosystem functioning

We explored the influence of the number of simulated species on model productivity and aboveground biomass. To this end, we performed simulations differing in the original number of species (S=2, 5, 10, 50, 100 species) and composition. For each diversity level S, we ran a hundred simulations, by randomly picking a combination of species each time. We then recorded the contribution of each species to the total aboveground biomass, AGB_s, and gross primary productivity, GPP_s, where s runs among the simulated species. These values were averaged over the full last simulated year. We also conducted simulations with monospecific stands for each of the 163 species parameterized in the model and recorded the simulated total aboveground biomass $AGB_{mono,s}$ and gross primary productivity $GPP_{mono,s}$.

We then quantified the net biodiversity effect on AGB and GPP, denoted ΔAGB and ΔGPP respectively, for each of the simulations. These net biodiversity effects are defined as

the difference between the simulated values and expected value under the null hypothesis that there is no effect of biodiversity, i.e. ecosystem process Y for the mixed-species forest equals the weighted sum of that in monocultures (Loreau and Hector 2001) :

$$\Delta Y = \sum_{s=1}^{N} Y_s - \sum_{s=1}^{N} w_s \times Y_{mono,s} \tag{30}$$

where Y is either AGB or GPP, w_s is a weight proportional to the regional species abundance (i.e. f_{reg}) such that $\sum_s w_s = 1$. For each simulation we partitioned the net biodiversity effect into two effects: $\Delta Y = CE_Y + SE_Y$ (Loreau and Hector 2001). The first term is the *complementarity* effect (CE_Y), which results from interspecific interactions (eg. facilitation or competition) or niche partitioning. The second term is the *selection* effect (SE_Y) and results from the dominance of selected species with particularly efficient traits either for biomass uptake or for carbon assimilation. We tested if species richness S had a positive effect on the net biodiversity effect, and for complementarity and selection effects separately (one-tailed t-test on ΔY, CE and SE). We also explored these effects using a one-way ANOVA with species richness as a fixed factor. Post-hoc pairwise comparisons were investigated using a Tukey HSD test. If needed to meet the assumptions of normality, ΔY, CE_Y and SE_Y were square-root transformed while preserving positive and negative signs (Loreau and Hector 2001, Morin et al. 2011).

Biodiversity effect on ecosystem functioning may result from the functional properties of species assemblages, partly independently to changes in species richness *per se*. Given a species richness S, the assemblage can present different trait statistics, and these in turn may induce selection or complementarity effects. To further interpret biodiversity effects, we thus computed continuous functional trait means (FM) and functional trait diversity indices (FD; Laliberté and Legendre 2010, Morin et al. 2011) for a set of traits for each simulation. We computed both FM and FD trait-by-trait and regressed Y, ΔY, CE_Y and SE_Y against FM and FD across simulations. Light availability is the only resource whose limitation is explicitly modeled in this version of TROLL, so we expected that the following traits would have a major effect: traits involved in light interception efficiency, such as leaf mass per area (LMA), shade-tolerance, such as the light compensation point (LCP) or light niche partitioning, such as maximal adult plant height (h_{max}; Westoby 1998, Poorter et al. 2009). As wood density underlies growth potential per investment (see eq. 15) and mortality (see eq. 23), we also included wood density as a potential predictor of biodiversity effects. For each of these four traits and for each simulation, FM and FD were computed as the weighted sum of species traits and of the species trait distance to the trait mean, respectively. In both cases, we used

species relative abundance as weighting factors (including individuals dbh ≥10cm). We also used relative AGB as species weights in FM and FD, but the results were similar and were not reported here.

Results

Simulating forest regeneration

Cross-run variability was low for the 500-yr simulation (Figs. 2-5), and below we report results for the median and range across the 100 simulations.

Fig. 2. Simulated forest structure, during a 500-year-long forest regeneration, starting from bare soil, with a monthly timestep and a constant external seed rain. Changes during the simulated regeneration of (A) stem densities of trees with a dbh ≥ 10 cm (in stems/ha); (B) stem densities of trees with a dbh ≥ 30 cm (in stems/ha); (C) aboveground biomass (in tons/ha); (D) mean wood density of the simulated tree community (in g/cm^3). The solid black line corresponds to the median while the shaded grey area represents the range across 100 simulations. Circle symbols correspond to the observed early-regeneration values, square and triangle symbols to the Paracou and Nouragues mature forest values, respectively.

Simulated stem density of trees with a dbh $\geq$ 10 cm displayed a sharp increase early on in the forest regeneration. Comparison with empirical measurements in a successional plot suggests that the simulation slightly overestimated stem density. After 500 years of simulation, stem density was of 493 trees/ha (N_{10}; range [474, 511] trees/ha), in good agreement with empirical data (Fig. 2A). Focusing on trees $\geq$ 30 cm dbh (N_{30}), we also found a good match between observed and empirical data both during the early successional dynamics and for mature forests (102 trees/ha, range [98, 106] trees/ha; Fig. 2B). Simulated AGB increased more slowly than N_{10} and N_{30}, and had barely reached stability after 500 yrs of regeneration (Fig. 2C), even though wood density reached a plateau after 100 years (Fig. 2D). The long-term simulated AGB was of 332 Mg/ha (range [321, 348] Mg/ha; Fig. 2C) within the range of AGB values reported for mature tropical forests worldwide (Chave et al. 2008a) and at the lower end of the range reported for mature forests in French Guiana (Chave et al. 2008b, Rutishauser et al. 2010). At 500 years, the forest presented structural features similar to the ones observed empirically. Ground-level LAI reached 6, and leaf distribution was homogeneous from 8 to 30 m (Fig. 3A). The diameter-size distribution declined exponentially, and the largest trees reached 150 cm dbh (Fig 3B).
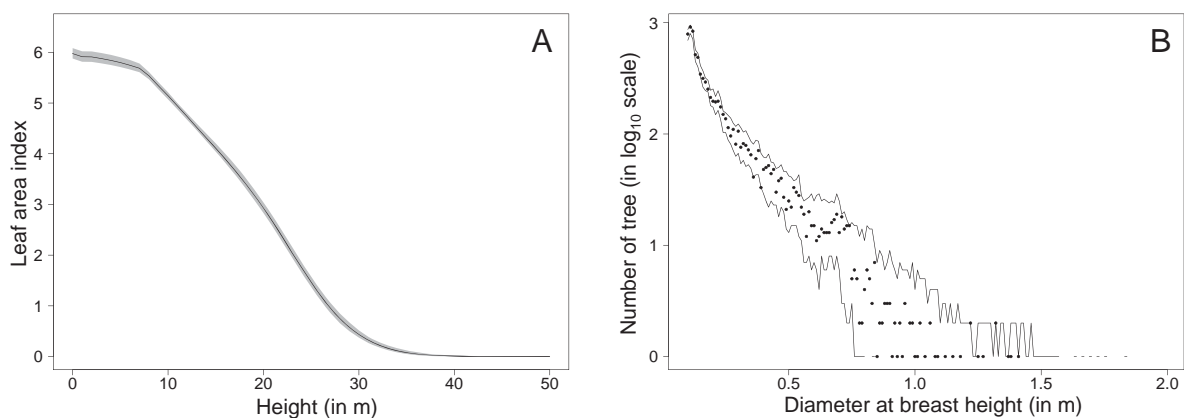
Fig. 3. Simulated mature forest (A) mean of the leaf area index as a function of height (in m). The black line corresponds to the median while the shaded grey area represents the range across 100 simulations. (B) dbh-size class distribution (dbh in m), for all trees with dbh $\geq$ 10 cm, in $\log_{10}$ scale. Points represent a typical simulation and the black lines represent the range envelope. Both panels were drawn for the simulated forest after 500 years of regeneration.

Gross primary productivity (GPP) stabilized within ca. 40 years, at 46 MgC.ha.yr^{-1} (range [45, 47] MgC.ha.yr^{-1}), a value slightly higher compared with those estimated empirically in Amazonian forests (Fig. 4A). The partitioning of GPP between autotrophic respiration and net primary productivity was also in agreement with empirical studies (Bonal et al. 2008, Aragão et al. 2009, Malhi 2012). Simulated leaf fall increased sharply in the first

5 years of the regeneration then stabilized quickly at 4.5 MgC.ha.yr^{-1} (range [4.45, 4.6] MgC.ha.yr^{-1}), within the range of leaf fall annual means observed empirically at our sites (Fig. 4B). The model however displayed less seasonal variability than observed empirically (Chave et al. 2008b, 2010).
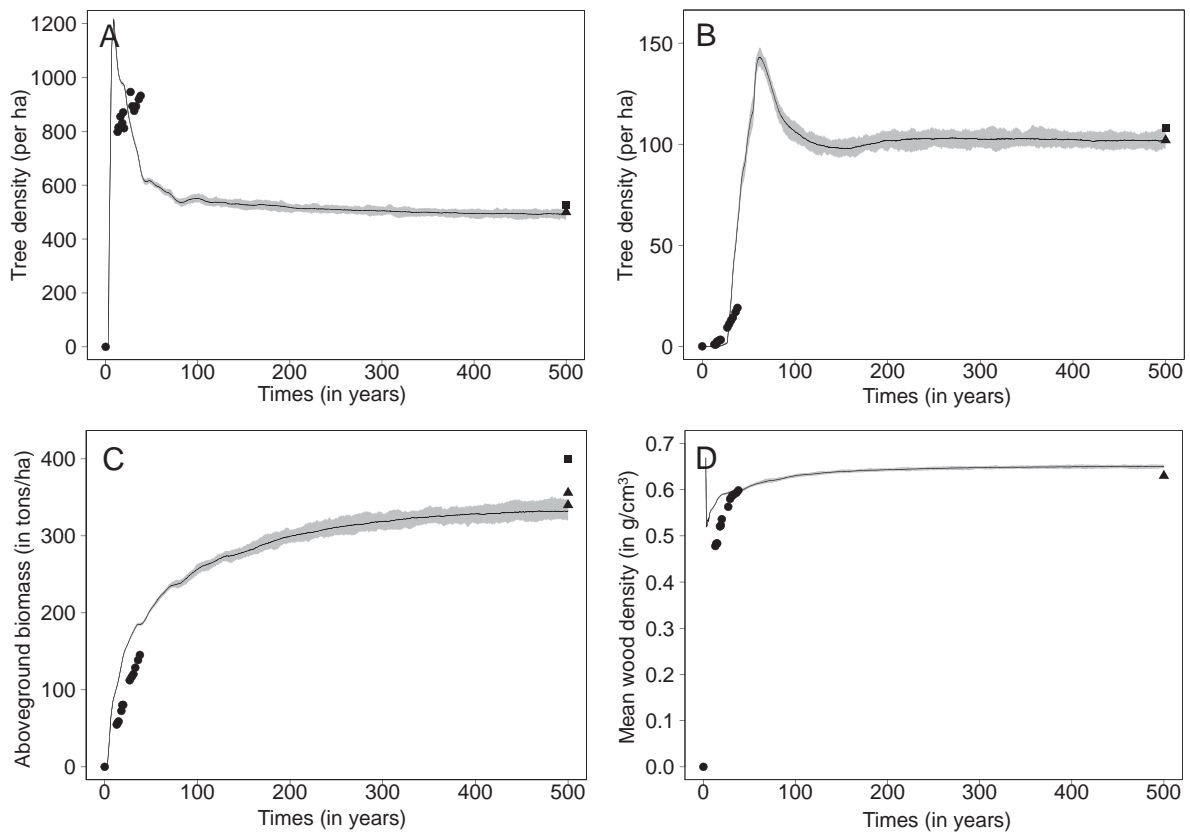

Fig. 4. Carbon flux, during a 500-year-long forest regeneration, starting from bare soil, with a monthly timestep and a constant external seed rain. (A) Dynamics of gross primary productivity (GPP) and its partitioning between net primary productivity (NPP), maintenance and gross respiration (R$_{maintenance}$ and R$_{growth}$; all in MgC ha^{-1} year^{-1}). The triangle corresponds to a GPP estimate from eddy-flux tower measurements at the Paracou research station (Guyafux, Bo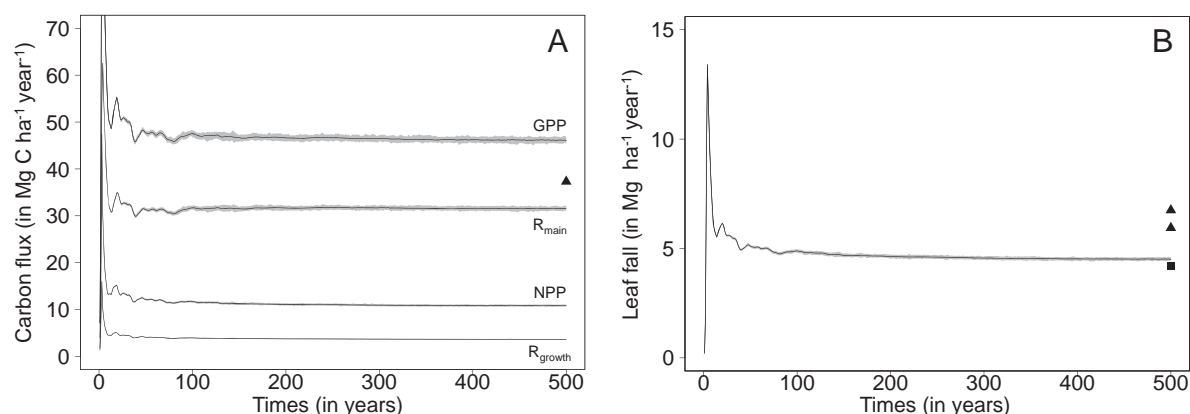nal et al., 2008; Malhi, 2012). (B) Dynamics of leaf fall (in Mg dry mass ha^{-1} year^{-1}). Square and triangle symbols correspond to the Paracou and Nouragues mature forest measurements, respectively (Chave et al. 2010). In both panels, the solid black line corresponds to the median and the shaded grey area represents the range across 100 simulations.

Simulated species relative abundances presented a clear shift in community composition during the succession (Fig. 5A), as is typically observed during natural secondary forest regeneration (Chazdon et al., 2010; Feldpausch et al., 2007; Lasky et al., 2014). Pioneer species, like *Cecropia obtusa* Trécul (Urticaceae) or *Laetia procera* (Poepp.) Eichler (Salicaceae), with high growth rates, light wood, and high mortality rate, dominated the community at the early stage of the regeneration. Later-stage successional species with denser wood, such as *Pouteria guianensis* Aubl. or *Micropholis cayennensis* T.D.Penn. (Sapotaceae) increased in dominance in the community. *Laetia procera* kept a relatively high density at the end of the simulated regeneration (Fig. 5A), even though this species is rare in old-growth forests of the Guianas (ter Steege et al. 2013). The species rank-abundance distribution after 500 years of regeneration showed the expected L-shaped profile (Rosenzweig 1995, Fig. 5B). The inverse Simpson diversity index was lower during the first decades of the regeneration, reached a transitory maximum after ca. 150 years of regeneration, and then slightly decreased and stabilized (Fig. 5C).
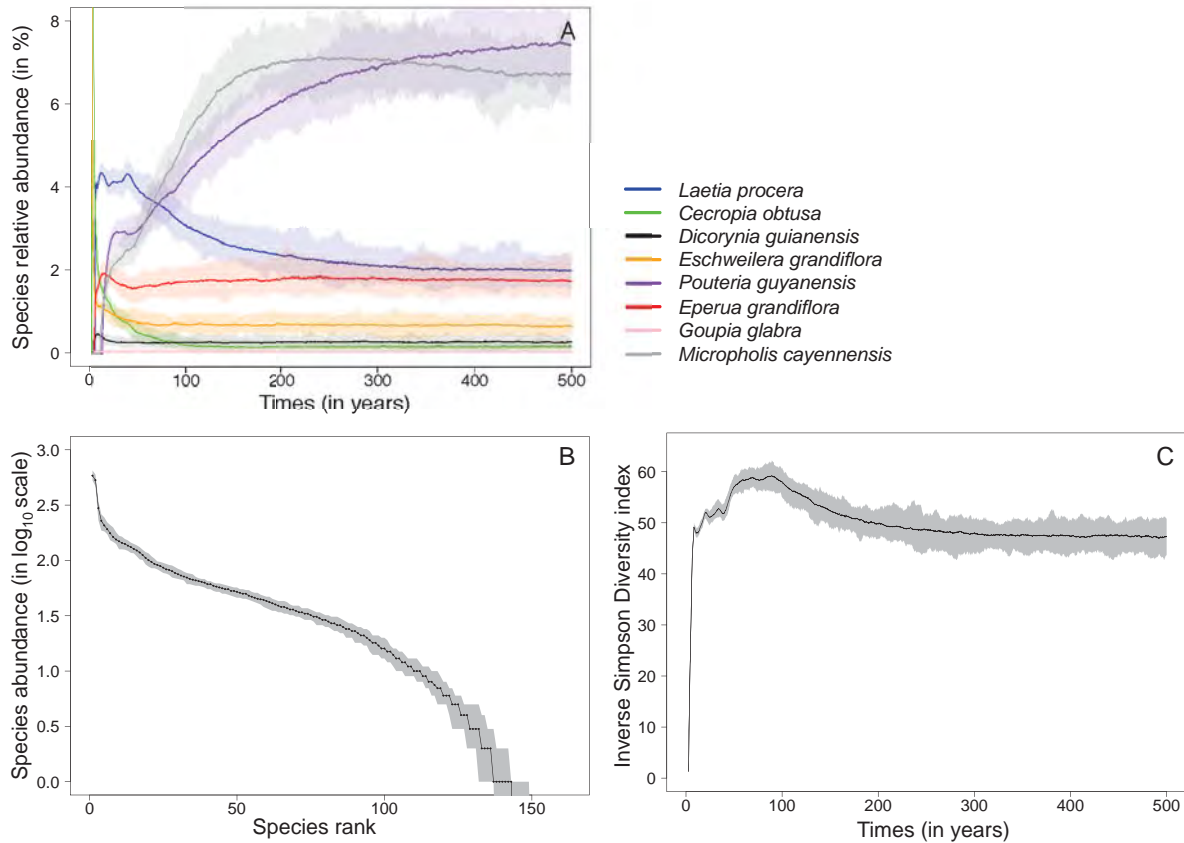
Fig. 5. Tree community diversity, during a 500-year-long forest regeneration, starting from bare soil, with a monthly timestep and a constant external seed rain. (A) Relative abundance trajectories during the regeneration for a subset of 8 species, known to have contrasting ecology and life history. (B) Species rank-abundance distribution of the simulated forest after 500 years of regeneration. (C) Temporal change of the Inverse Simpson Diversity (ISD) index of the simulated tree community (dbh ≥ 10cm), computed as the reciprocal of the sum of square of species relative abundances (a higher ISD means a higher diversity). The solid black line corresponds to the median and the shaded areas represent the range across 100 simulations.

Sensitivity analysis

To assess the robustness and identify the main drivers of our results, we performed a sensitivity analysis on five of the global parameters, k, ϕ, f_{wood}, f_{canopy} and m. These parameters had a strong influence on almost all outputs of the mature forest (Fig. 6) or in the early phase of the regeneration (Fig. 7). We also tested the sensitivity of g_1, and found that it did not have any significant influence on the simulation results within the empirical ranges reported for this parameter (Lin et al. 2015).

A larger ϕ value and a smaller k value resulted in a larger GPP, AGB and LAI (Fig. 6), and in an increase of stem density and AGB at the early stage of regeneration (higher RMSE values, Fig. 7). The ratio k/ϕ, had the strongest effect of all tested parameters (Fig 6).

k/ϕ tightly constrained the whole process of light diffusion, absorption and conversion into assimilated carbon.
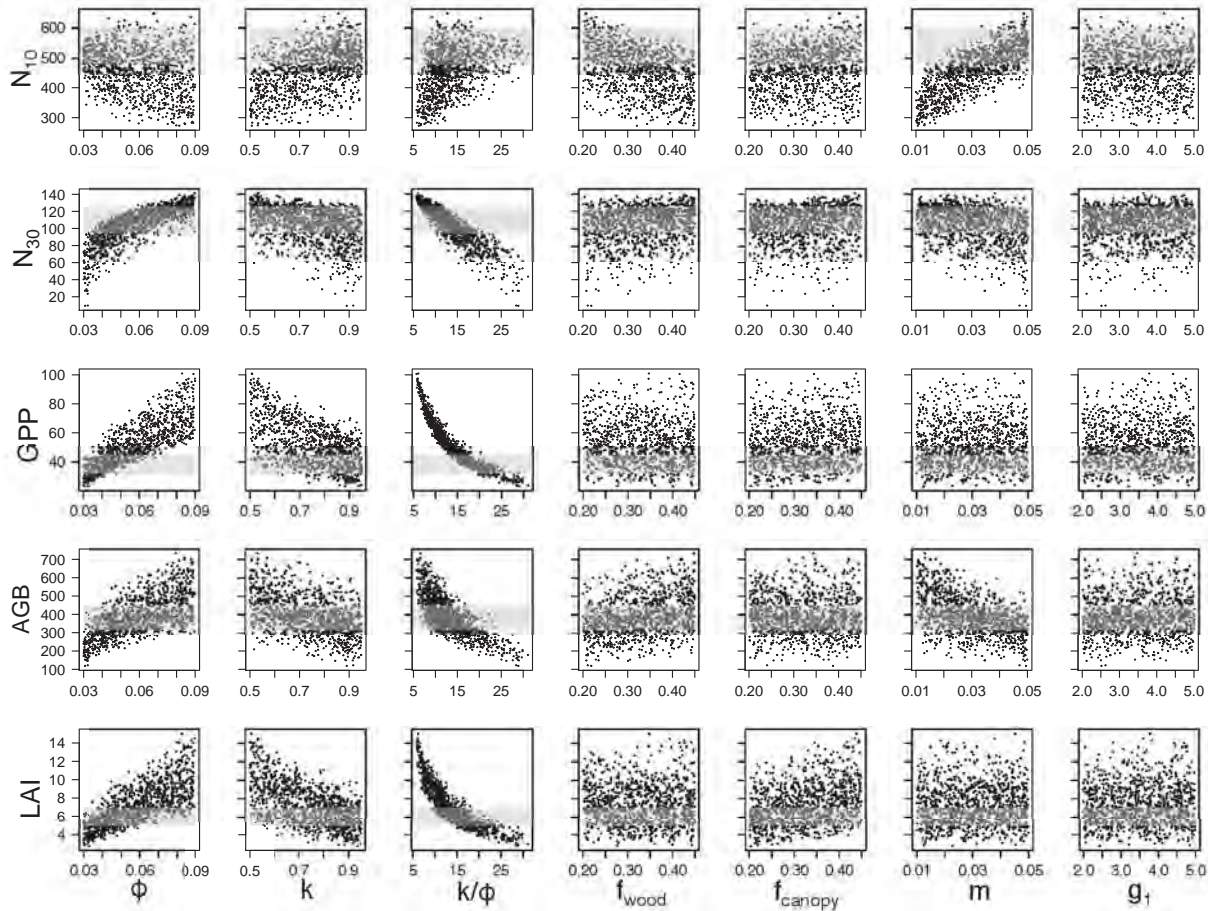
Fig. 6. Influence of parameter variation on mature forest characteristics simulated by TROLL, as revealed by a sensitivity analysis (1000 independent simulations) varying six parameter values (ϕ, k, f_{wood}, f_{canopy}, m and g_1) randomly and independently (Table 2). Each point corresponds to one 500-year simulation (with monthly timestep), and outputs were averaged over the 20 last iterations. Outputs are plotted on the y-axis, with, from top to down lines: stem densities of trees with dbh $\geq$ 10 cm (N_{10}, in stems/ha); stem densities of trees with dbh $\geq$ 30 cm (N_{30}, in stems/ha); gross primary productivity (GPP, in MgC ha^{-1} year^{-1}); aboveground biomass (AGB, in tons/ha); leaf area index (LAI). Parameter values are plotted on the x-axis, with, from left to right columns: apparent quantum yield for C fixation (ϕ, in molC/mol*photons*); light extinction coefficient (k); k/ϕ ratio; fraction of NPP allocated to wood growth (f_{wood}); fraction of NPP allocated to canopy (f_{canopy}); maximal basal mortality rate (m); stomatal conductance parameter (g_1, in kPa$^{1/2}$). Grey bands indicate ranges of realistic output values, as revealed by empirical studies.

Allocation parameters also had a notable influence on the simulated results. A larger fraction of NPP allocated to wood (f_{wood}) resulted in a higher AGB, increasing the number of large trees at the expense of smaller ones (Figs. 6-7), while a larger allocation to canopy (f_{canopy}) resulted in a denser foliage (higher LAI, Fig. 6). The parameter m, which controls the background stem mortality rates, had a strong effect on stem density and size. Smaller values of m induced a higher density of large trees and less smaller trees. As a result, it strongly impacted AGB, but had a limited impact on GPP (Fig. 6).
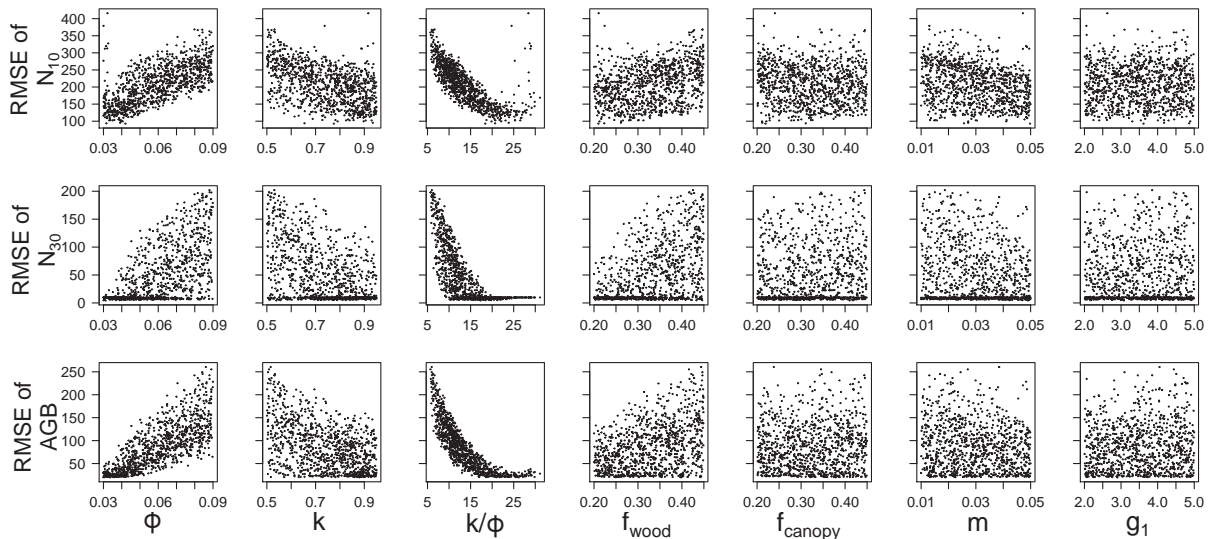
Fig. 7. Influence of parameter variation on early regeneration dynamics simulated by TROLL, as revealed by a sensitivity analysis as in Fig. 6. Each point corresponds to one 500-year simulation (with monthly timestep), showing the root-mean-square errors (RMSE) of outputs with the corresponding values observed in a secondary forest inventory. Output RMSE are plotted on the y-axis, with, from top to down lines: RMSE of stem densities of trees with dbh $\geq$ 10 cm (N_{10}, in stems/ha); RMSE of stem densities of trees with dbh $\geq$ 30 cm (N_{30}, in stems/ha); RMSE of aboveground biomass (AGB, in tons/ha). Parameter values are plotted on the x-axis, with, from left to right columns: apparent quantum yield for C fixation (ϕ, in molC/mol*photons*); light extinction coefficient (k); k/ϕ ratio; fraction of NPP allocated to wood growth (f_{wood}); fraction of NPP allocated to canopy (f_{canopy}); maximal basal mortality rate (m); stomatal conductance parameter (g_1, in kPa$^{1/2}$).

GPP and AGB were positively correlated but weakly so across the simulations (Fig 8). The slope of the relationship was strongly controlled by m and f_{wood} (Fig. 8B-C), whereas the k/ϕ ratio determined the values of the simulated GPP and aboveground biomass along these slopes (Fig. 8A). A lower m or a larger f_{wood} resulted in a larger AGB increment for a given increase in productivity (Fig. 8B-C). GPP and LAI were tightly and linearly correlated, both decreasing with k/ϕ (Fig. 8E). Various allocations to canopy explained the major part of the scatter in the linear relationships, a higher f_{canopy} resulting in a larger LAI for a given GPP (Fig 8H). An increase in N_{30} led to an increase in AGB below ca. 350 tons/ha, above which threshold N_{30} saturated while AGB kept increasing (Fig. 8I-J). N_{10} and N_{30} were negatively related. A lower m value led to both a higher N_{30} and a smaller N_{10} (Fig. 8N), whereas a lower k/ϕ led to more big trees (higher N_{30}) for a given N_{10} (Fig. 8M). The simulated forest basal area was tightly correlated with AGB across the simulations, and net primary productivity (NPP) to GPP (Appendix 3), so neither basal area nor NPP were discussed explicitly here.

The addition of negative density-dependence in the model resulted in an increase of the Inverse Simpson Diversity index of 59-87 % for trees with dbh$\geq$10cm for an increasing magnitude of density-dependence (α in [0.5, 2]) relative to the control (α=0, Fig. 9). The dominant species declined from 8% (α =0) to 2.5% (α=2) in relative abundance (Fig. 9). It

did not significantly affect ecosystem processes, with simulated GPP and AGB (with α>0) staying within the range of outputs obtained without negative density-dependence (α =0).
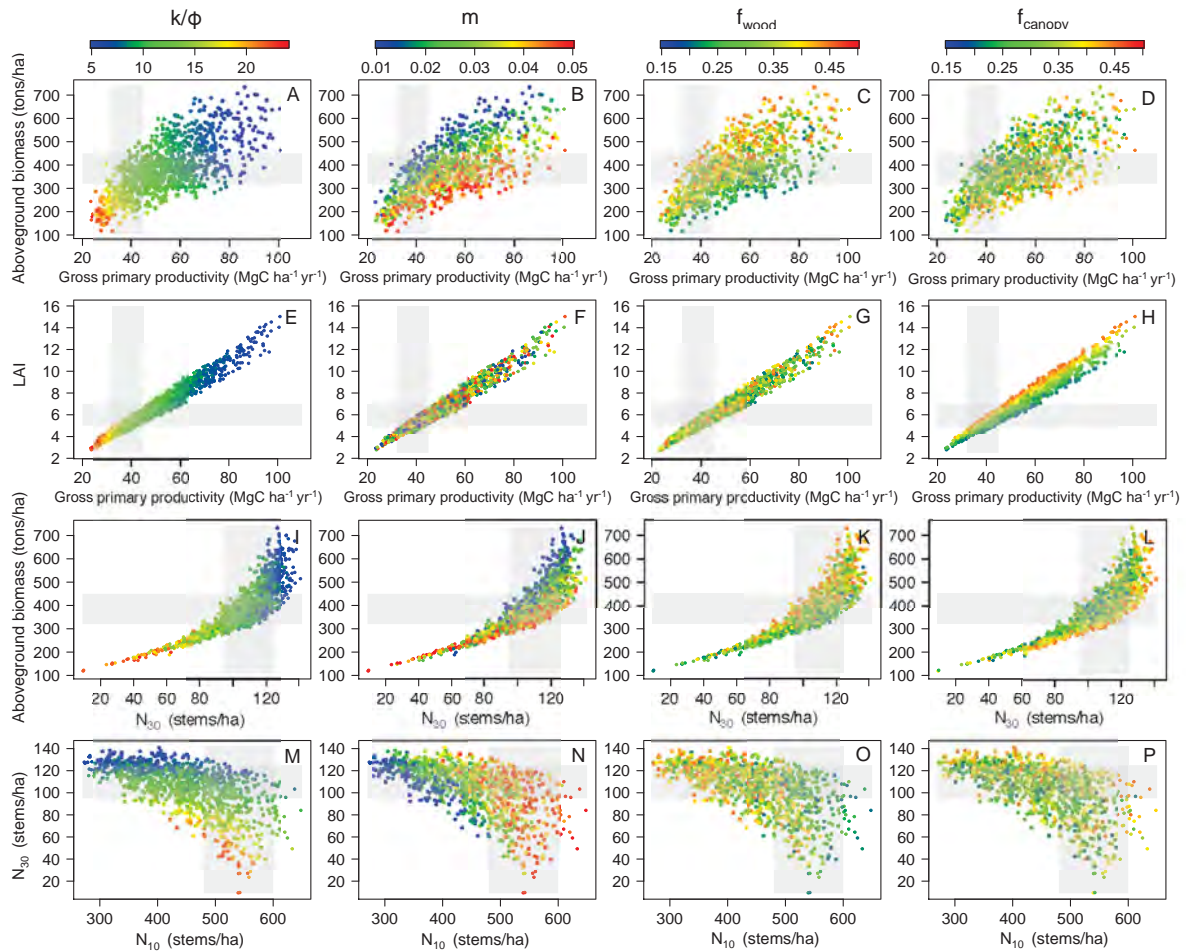
Fig. 8. Covariation of simulated forest characteristics and their dependence on parameter values, as revealed by a sensitivity analysis as in Fig. 6. Each point corresponds to one 500-year simulation (with monthly timestep), with the outputs averaged over the 20 last iterations. (A), (B), (C), (D): aboveground biomass (AGB, in tons/ha) as a function of gross primary productivity (GPP, in MgC ha^{-1} yr^{-1}); (E), (F), (G), (H): leaf area index (LAI) as a function of GPP; (I), (J), (K), (L): AGB as a function of stem density of trees with dbh $\geq$ 30 cm (N$_{30}$, in stems/ha); (M), (N), (O), (P): N$_{30}$ as a function of stem density of trees with dbh $\geq$ 10 cm (N$_{10}$, in stems/ha). In (A), (E), (I), (M), the covariation dependence on k/ϕ values is shown in colors; in (B), (F), (N), (E) on m; in (C), (G), (K), (O) on f$_{wood}$; and in (D), (H), (L), (P) on f$_{canopy}$. Grey bands indicate ranges of realistic output values, as revealed by empirical studies.

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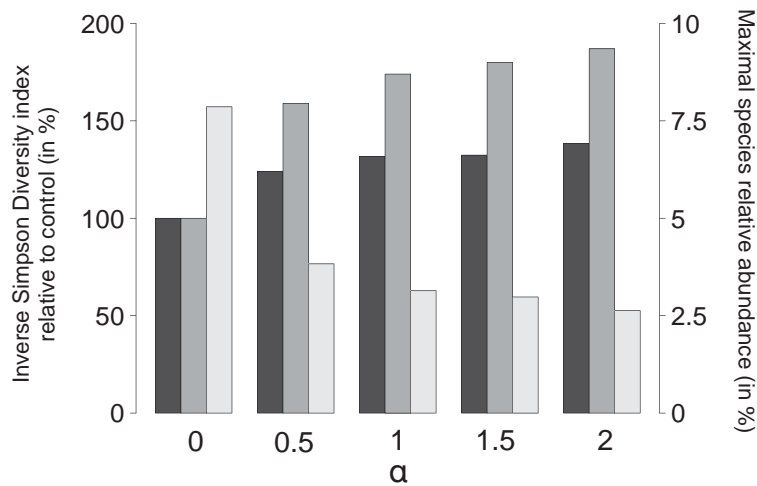
Fig. 9. Influence of simulated biotic negative density-dependence processes on community composition for different levels of magnitude of density-dependence processes (quantified by α, see Parameterization, validation data, and tests). The Inverse Simpson Diversity index for trees with dbh <10cm (black) and dbh ≥ 10cm (dark grey) relative to control (α=0), in % (left axis); and relative abundance of the most abundant species in the community (dbh>10cm; in %, right axis, light grey).

Biodiversity and ecosystem function

We tested the effect of biodiversity on simulated GPP and AGB by changing the simulated species richness and composition. The median GPP slightly increased with species richness, but this effect progressively leveled off above 10 species, and it was most variable across simulations for low-species assemblages (Fig. 10A). In single-species runs, long-term average GPP was 10.2-60.6 MgC ha^{-1}year^{-1}, and in two-species runs it was 24.4-56.7 MgC ha^{-1}year^{-1}, thus in some case it resulted in overyielding in comparison to simulations with 100 species and 163 species (Figs. 10A, 4A). The net biodiversity effect on GPP (ΔGPP) was significantly positive, but species richness explained only 15% of ΔGPP (Fig. 10B). The selection effect (SE$_{GPP}$) was also significantly positive (all p<0.0001, Fig. 10C). In contrast, the complementarity effect (CE$_{GPP}$) was much lower in magnitude although significantly positive at high species diversity (S=50 and 100; Fig. 10D). Thus, ΔGPP was predominantly driven by the selection effect SE$_{GPP}$. The linear regression between ΔGPP and SE$_{GPP}$ was strong (p<10^{-15}, R^2=0.98), with slope not significantly different from 1 and intercept not significantly different from 0.

The influence of species richness on AGB was less clear than for GPP, with strong variability across simulations (Fig. 10E, Table 3). The net biodiversity effect on AGB (ΔAGB) was weakly but significantly positive (Fig. 10F). Both selection effect (SE$_{AGB}$) and complementarity effect (CE$_{AGB}$) were also weakly significantly positive (p<0.05, except for SE$_{AGB}$ with 50 species, and CE$_{AGB}$ with 2 and 5 species; Figs. 10G-H).
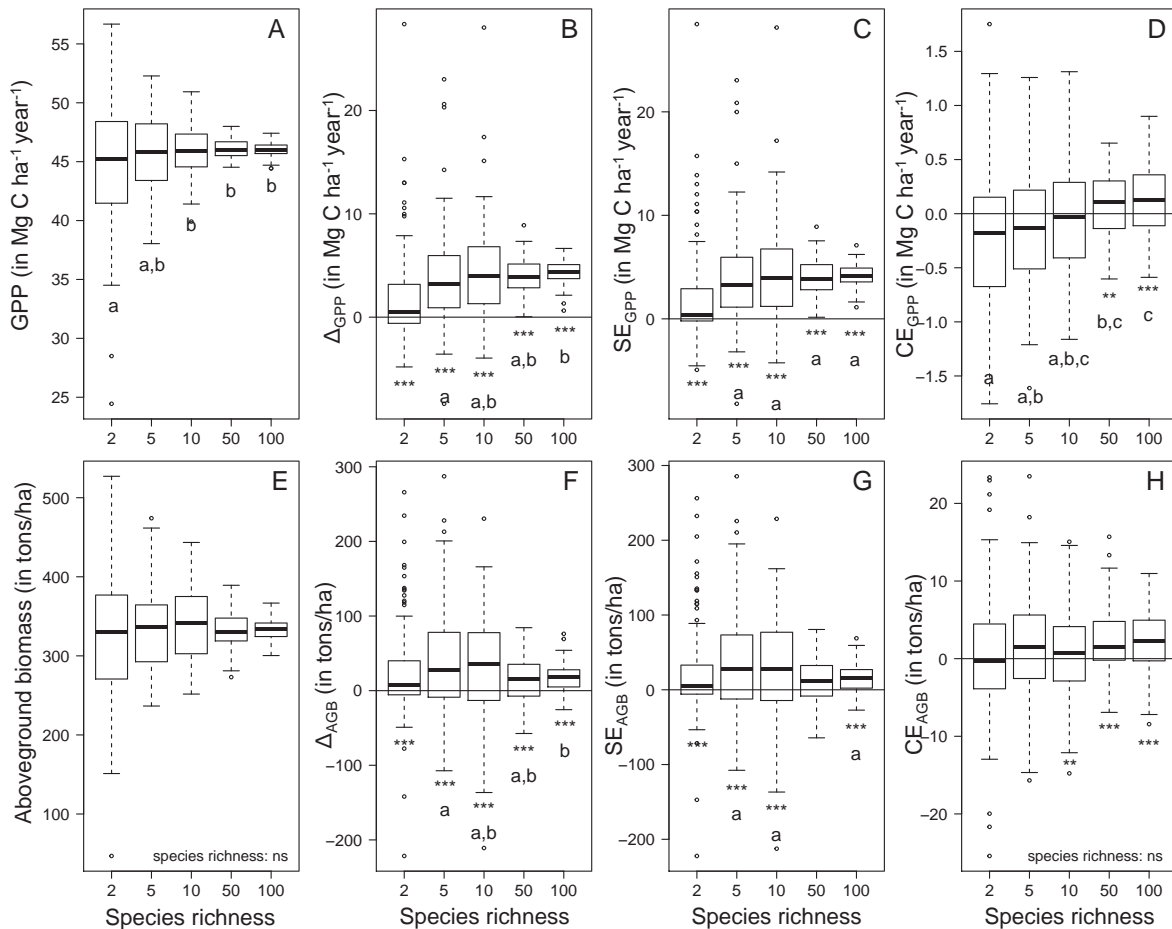
Fig. 10. Influence of species richness on simulated gross primary productivity (A; in MgC ha^{-1} year^{-1}) and aboveground biomass (E; in tons/ha), as well as on the biodiversity effects on both ecosystem properties (ΔGPP, B; ΔAGB, F) and their partitioning between complementarity effect (CE$_{GPP}$, C; CE$_{AGB}$, G) and selection effect (SE$_{GPP}$, D; SE$_{AGB}$, H). For each level of species richness (N=2, 5, 10, 100), boxplot of values of 100 simulations with randomly drawn species combinations among the 163 simulated species. Note the different y-axis scales. Horizontal black lines on biodiversity effect plots is the reference. Asterisks indicate significance on mean values (one-tailed t-tests, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$). In case of an overall effect of species richness (ANOVA; otherwise, ns), different lower case letters indicate a significant difference between species richness levels (post hoc Tukey HSD test, $p<0.05$).

Variability in the GPP of monocultures (GPP$_{mono}$) was positively related with mean LMA ($p<10^{-15}$, $R^2=0.71$) and LCP ($p<10^{-15}$, $R^2=0.66$), but was weakly related to h$_{max}$ ($p<0.001$, $R^2=0.07$) and not to wood density ($p=0.09$). Similarly, GPP of multispecific simulations was strongly positively correlated with FM$_{LMA}$ and FM$_{LCP}$, and in a lower extent with FD$_{LMA}$ and FD$_{LCP}$ (Table 3). Variability in the AGB of monocultures (AGB$_{mono}$) was explained by all four investigated traits ($p<10^{-10}$, $R^2 \in [0.23, 0.35]$). In multispecific simulations, AGB was primarily correlated with FM$_{wsg}$ ($p<10^{-6}$, $R^2=0.62$), and – to a lower extent – with FM$_{hmax}$ ($p<10^{-14}$, $R^2=0.11$, Table 3). Trait diversity did not influence AGB in multispecific simulations, or only weakly (Table 3). Overall, biodiversity effects on GPP and AGB were weakly explained by trait means and trait diversity. For all linear regressions of

ΔY, CE$_Y$, SE$_Y$ as dependent variables and FM and FD as independent variables we found a low coefficient of determination (R^2<0.1), except FD$_{wsg}$ that explained 20% of CE$_{GPP}$ (Table 3).

Table 3. Biodiversity and ecosystem functioning. Effect of species richness, community functional trait mean (FM) and diversity (FD) on simulated gross primary productivity (GPP) and aboveground biomass (AGB), and the biodiversity effects on GPP and AGB (ΔGPP and ΔAGB). Results were obtained from 500 simulations varying in species richness and composition, with randomly drawn combinations of N=2, 5, 10, 50 and 100 species among 163. ΔGPP and ΔAGB are defined as the difference between the simulated values and expected value under the null hypothesis that there is no effect of biodiversity. These effects are partitioned into a complementarity effect (CE$_Y$, with Y=AGB or GPP), which results from interspecific interactions or niche partitioning, and a selection effect (SE$_Y$), which results from the dominance of selected species with particularly efficient traits either for biomass uptake or for carbon assimilation. Test of species richness effect: one-way ANOVA with species richness as a fixed factor. Test of FM and FD effects: linear regression with FM and FD as independent variables. Four species-specific traits are explored: leaf mass per area, LMA; light compensation point, LCP; maximal adult plant height, h$_{max}$; and wood specific gravity (wsg). For each trait and each simulation, FM and FD were computed as the weighted sum of species traits and of the species trait distance to the trait mean, respectively. In both cases, we used species relative abundance as weighting factors (including individuals dbh $\geq$10cm). R^2 of models (n=500 simulations; *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$, ns: non-significant). R^2 above 0.10 are highlighted in bold.

	GPP				AGB			
	GPP	ΔGPP	CE$_{GPP}$	SE$_{GPP}$	AGB	ΔAGB	CE$_{AGB}$	SE$_{AGB}$
Species richness	0.03**	0.15***	0.05***	0.13***	ns.	0.02*	ns.	0.02*
Functional mean (FM)								
LMA	**0.66***	0.05***	0.01*	0.04***	0.04***	ns.	0.01*	ns.
LCP	**0.76***	0.04***	<0.01*	0.02***	ns.	ns.	ns.	ns.
hmax	0.01*	0.02***	ns.	0.02**	**0.11***	0.01**	0.02**	0.01*
wsg	0.02**	ns.	0.02***	ns.	**0.62***	0.08***	0.01**	0.08***
Functional diversity (FD)								
LMA	**0.20***	0.05***	0.04***	0.03***	ns.	0.01*	0.04***	0.02**
LCP	**0.14***	0.07***	0.03***	0.05***	ns.	0.01**	ns.	0.02**
hmax	0.04***	0.02**	ns.	0.02**	0.03***	ns.	0.08***	ns.
wsg	0.02**	0.02***	**0.20***	ns.	0.03***	0.06***	ns.	0.06***

Discussion

In this study, we describe and use an individual-based vegetation model parameterized for a tropical rainforest of Amazonia, to simulate the forest successional dynamics. The outcomes of the simulations were then compared with empirical data. We also performed a sensitivity analysis on some of the main model parameters to explore the robustness of our predictions regarding lesser-known model parameters, but also to explore the drivers of ecosystem processes, structure and composition given environmental conditions. Finally, we used a unique feature of this model, the ability to parameterize many species within the same community based on relatively few key parameters, to investigate the effects of species and functional diversities on simulated ecosystem processes. Here we discuss the implications of our findings.

Successional dynamics

The regeneration dynamics as simulated by TROLL were comparable with the ones observed empirically. We compared the model outcomes to field data for stem numbers, aboveground biomass, and productivity. The data-model consistency, as well as the relatively low part of variability due to demographic stochasticity, suggest that the modeled forest succession is primarily conditioned by the proximity to mature forests and their dispersers (Norden et al. 2009). Norden et al. (2015) emphasized the idiosyncratic nature of forest regeneration in the Neotropics, and predicted that stochasticity may be as important as determinism in forest regeneration. Here we were able to identify key mechanisms and forest community's properties that mostly influence regeneration and forest ecosystem processes and composition given environmental conditions and constant seed rain. TROLL could be used to quantify the influence of the spatial structure of the seed rain on the early stages of the assembly of a regenerating rainforest (Köhler et al. 2003). We predict that the relative role of stochasticity in forest regeneration with be largely conditioned by the intensity of the seed rain and its species composition (Chazdon 2003).

The recovery dynamics of AGB was slow due to the progressive shift in composition during the regeneration with fast-growing early successional species with low wood density being progressively replaced by later successional species with higher wood density

(Rozendaal and Chazdon 2015). The slow growth and size gain of the latter induced an increase in AGB even after a stabilization of community-wide mean wood density. It would be interesting to explore whether TROLL is able to capture the cross-site variability in AGB recovery rates, due to variation in floristic composition alone. Slow AGB recovery rate have already been observed in forest chronosequences (Saldarriaga et al. 1988). This suggests that even though tropical forests are quick to store AGB within the first decades of regeneration, reaching equilibrium in AGB takes a very long time, typically several centuries. The simulated AGB recovery at 20 years was 143 Mg/ha, comparable with a recent compilation of AGB recovery rates for Neotropical forests (mean of 122 Mg/ha; Poorter et al. 2016). However, the rate of recovery quickly slowed down, with an additional 42 Mg/ha recovered from 20 and 40 years. The plot reached 80% of the maximal AGB stock in 115 years, and 90% in slightly less than 200 years. Another remarkable feature is that 50-130 years after the start of recovery, our simulated area still accumulated between 0.5 and 2 $Mg.ha^{-1}.yr^{-1}$ of AGB. This in within the range of AGB gains reported over Amazonia (Brienen et al. 2015), and suggests that disturbances have a long-term legacy on forest AGB stocks (Chave et al. 2008a).

The recovery dynamics was also quantified in terms of the number of trees ≥ 10 cm dbh, which showed a slightly too early overshooting of tree density up to 1200 trees/ha in the simulated data, followed by a leveling at around 500 trees/ha, both figures consistent with field data (Feldpausch et al. 2007, Chave et al. 2008b, Rutishauser et al. 2010; Fig 2). For trees ≥ 30 cm dbh, we also observed a slightly too rapid response of the simulated trees, consistent with the overestimation of simulated AGB, compared with empirical data. We emphasize that these results were obtained without fine-tuning any of the parameters, and that reproducing the trajectory of both stem density and AGB is difficult as this transient dynamics is likely to be affected by a number of factors, among which soil compaction and nutrient availability, the physiology of pioneer species and microclimatological condition in a young regrowing forest (see below).

Carbon fluxes stabilized within the first decade of simulation, also consistent with empirical expectation, even though in situ data on forest fluxes are still missing for regenerating tropical forests (Fig. 4). Constraining the GPP estimates for the tropical forest biome is a difficult challenge (Beer et al. 2010, Jung et al. 2011), and the estimates reported here are within the range of variability reported for tropical forests. We also note that even if the LAI as simulated here was consistent with observations, TROLL was unable to reproduce

the strong seasonal pattern in leaf fall dynamics, as observed in Amazonia (Chave et al. 2010, Wu et al. 2016).

Sensitivity analysis

We sought to assess the implications of varying some global model parameters across their observed range of variability on the model outputs. The simulations spanning a range of parameter values always included empirically realistic outputs when considering final (+500 yrs) values of AGB, LAI, GPP, N_{10} and N_{30} as summary statistics. This sensitivity analysis also sheds light on the effect of some parameters that were assumed invariant across species and independent of environmental conditions, because a detailed description is lacking for them. However, it is known that, for instance, the light extinction factor k varies with leaf angle, hence with height within the canopy and species (Meir et al. 2000, Kitajima et al. 2005). Likewise, ϕ should vary with leaf thickness and leaf light exposure (Long et al. 1993, Poorter et al. 1995). Mortality rate and allocation patterns are also expected to vary among species strategies and individual local environments, resulting in different tree architecture and light and element acquisition (Iida et al. 2011, 2012). The strong model sensitivity to these parameters we found here is in agreement with our assumptions and with other existing modeling studies that explored it (Medlyn et al. 2005, Mercado et al. 2009b). Variability and uncertainties in these parameter values are underexplored empirically even though they are widely used by vegetation models. It would be important to further explore this question with field data.

The simulations made in this sensitivity analysis illustrated that modeled GPP and AGB are not directly related (Fig. 8A). Lower species stem mortality rates (m) or bigger allocation of productivity to wood growth (f_{wood}) induced a larger biomass for a given productivity. The overall low relationship between GPP and AGB illustrates the fact that multiple processes shape the pathway of assimilated carbon by photosynthesis toward standing living biomass. AGB is tightly related to NPP multiplied by residence time (one divided by death rate), while NPP is tightly related to GPP times allocation into tissue (Malhi 2012). Better estimates of ecosystem-wide residence times and allocation, as obtained from empirical studies (Johnson et al., 2016; Litton et al., 2007; Malhi et al., 2015) would help better constrain the model. Observations across Amazonian forests have shown that stem mortality rates is a strong predictor of AGB, consistent with the view that stand-size structure determines AGB, but that productivity was a poor predictor of aboveground biomass

(Johnson et al. 2016). If our results are interpreted as simulations spanning the substantial range of stem mortality resulting from variation in environmental conditions and floristic composition over Amazonia, our analyses are in support of these observations. Also, the contrasting biomass stocks found in sites with similar productivity might be controlled by different allocation patterns, that may be driven by climate and soil composition and structure (Quesada et al. 2009, 2012, Doughty et al. 2014, Malhi et al. 2015).

Variation in light absorption across sites may also explain the observed difference in the effect of stem mortality rate on AGB (Johnson et al. 2016). Indeed, the whole process of light diffusion, absorption and the resulting carbon uptake by photosynthesis, which were constrained by the k/ϕ ratio, drove productivity and biomass independently of stem mortality and allocation processes. The major predictor of GPP variation was LAI, as has been found in previous global syntheses (Beer et al. 2010; Fig. 8I). A more efficient light diffusion and conversion to carbon (lower k/ϕ) allowed more dense and packed canopies to develop, with more large trees and higher LAI.

Our model of stomatal conductance is based on a recent advance in theory (Medlyn et al. 2011, Prentice et al. 2014). Considering the importance of stomatal conductance and internal CO_2 concentration in driving water use efficiency and productivity, we expected the model to be sensitive to the main parameter g_1. However, the model outputs presented no clear trends with g_1, although the chosen range of g_1 values spanned the range of reported values (Lin et al. 2015; Table 2). Within this range and given the VPD and temperature amplitudes at our sites, variation in carbon assimilation due to changes in g_1 is actually limited (see Appendix 4 for an illustration). Alternative model of stomatal conductance with different sensitivities to VPD have been found to yield similar performance for tropical evergreen forests (Knauer et al. 2015). We also tested a dependence of g_1 as a function of wood density, as suggested in Lin et al. (2015, see Fig. 3 therein). This change in the model did not really improve its performance (results not shown), unsurprisingly considering the weak explanatory power of the relationship.

In tropical ecology, it has long been established that one of the foremost process driving the abundance of species, the maintenance of rare species, and indirectly ecosystem processes, is the so-called Janzen-Connell hypothesis (Janzen 1970, Connell 1971). Because we aimed at jointly modeling ecosystem processes and biodiversity, our sensitivity analysis also included a test of the hypothesis that negative density-dependence (the competitive advantage of rare species over abundant ones) could alter community structure and also regulate plant productivity (Terborgh et al. 2001, Schmitz 2003). In agreement with theories

as well as observations and experimental studies (Wright 2002, Uriarte et al. 2004, Gonzalez et al. 2010, Bagchi et al. 2014), we found an increase in community diversity (evenness) due to negative density dependence, an effect that increased through life stage. Adding such effect in vegetation models may be increasingly important under the potential strong environmental filtering and resulting change in floristic composition already observed and expected to occur under climate change (Meir et al. 2015, Feldpausch et al. 2016, van der Sande et al. 2016).

Biodiversity and ecosystem functioning

By simulating ecosystem processes while keeping track of species identity of individuals, we could investigate the link between biodiversity and ecosystem functioning (BEF). BEF relationships have been intensely studied over the last decades, through experiments (Cardinale et al. 2009), observations along natural gradients of species richness (e.g. Paquette and Messier 2011, Grossiord et al. 2014) or theory (e.g. Loreau 1998, 2010). Experimental studies have often been limited in time scale and to low species richness. Studies have predominantly focused on grasslands and to a lower extent on temperate forests (but see Potvin and Gotelli 2008, Lohbeck et al. 2015, Poorter et al. 2015). By virtually manipulating the number and identity of species, we assessed the effect of species richness and functional composition on the simulated productivity and aboveground biomass of a tropical forest plot. As expected, species richness had a positive effect on both ecosystem characteristics (Hooper et al. 2005), even though, as already observed, this effect leveled off at high species richness for productivity (Grime 1997) and was weak for aboveground biomass (Chisholm et al. 2013). The contrasting effect of species richness on GPP and AGB, and their weak relationship, emphasize the need to explore these ecosystem metrics separately, rather than by using one as a surrogate of the other (Chisholm et al. 2013).

Species richness alone explained a small fraction of the GPP and AGB variability across simulations. We were able to simulate the influence of biodiversity at a much larger spatial scale than any typical experimental and natural set-ups. In agreement with our results, biodiversity effect may vanish with increasing spatial scale, as found empirically in a range of tropical forests (Chisholm et al. 2013). Also, we observed a strong variability for a given species richness, showing that species identity and composition largely control ecosystem properties. Functional traits are known to vary not only across species by also across sites (Fyllas et al. 2009, Baraloto et al. 2010, Banin et al. 2012), and our result suggests that it would be important to use site-specific traits to simulate ecosystem functioning (ter Steege et

al. 2006, Quesada et al. 2012, Fyllas et al. 2014). This remains a challenge because spatial variability in trait values is still poorly represented in vegetation models (de Almeida Castanho et al. 2016, Johnson et al. 2016).

Also in simulations with low species richness, we found particularly contrasted ecosystem properties. The best way to assess whether these patterns bear some reality would be to contrast the ecosystem functioning in old-growth forests with that of monospecific plantations. In French Guiana, experimental monospecific plantations of 16 species have been established in the early 1980s (Roy et al. 2005, Bréchet et al. 2009). Bréchet et al. (2009) showed that litterfall, a reasonably good proxy for NPP in tropical forests (Malhi et al. 2011), presented a four-fold variation across the 16 monospecific plantations, and that basal area – a good proxy for AGB – showed a 10-fold variation. This demonstrates that tropical tree species, when grown alone, do display the large range of variation in the ecosystem properties we examined.

The major impact of species diversity on productivity in our simulations was the selection effect – the influence of a selective group of species on the ecosystem, rather than a complementarity effect between species niches in resource acquisition. This finding contrasts with some empirical studies where a stronger complementarity than selection effect was evidenced (Loreau and Hector 2001), but is in agreement with a stronger effect of community-weight trait means than niche complementarity observed in a tropical forest (Chiang et al. 2016). In our simulations, ecosystem productivity and biomass were overall much better explained by community functional trait means than by functional diversity. We found complementarity effect to be positive only above a high S value, suggesting that complementarity might not be a key factor in species-poor communities. Our model does not include any other resource limitation than light, hence it is difficult to exclude that including other limitations, especially those mediated by nutrient availability, may significantly alter the results. In that sense, our results should be interpreted as a null scenario against which to test additional processes. For instance, it would be interesting to test how the addition of a nitrogen-phosphorus cycle would yield different outcomes, as, in tropical forests, plants have various nitrogen and phosphorus uptake strategies (Wright et al. 2011, Barantal et al. 2012, Batterman et al. 2013).

The clear positive selection effect on productivity involving both species leaf mass per area and light compensation point indicates that productivity is strongly driven by both leaf lifespan (Reich et al. 1992), hence LAI, and leaf productivity (Falster et al. 2011). Similarly, wood density correlates with residence time, hence biomass accumulation (Falster et al.

2011). These results agree with our sensitivity analyses. Also, in natural tropical forest communities, asynchronous leaf phenology may lead to complementarity effect through temporal niche partitioning (Reich et al. 1992, Sapijanskas et al. 2014), but this effect is not included here as mechanistic drivers of aseasonal leaf demography in tropical evergreen rainforest remain poorly known.

Perspectives in forest modeling

The current version of TROLL offers several novelties over previous models of the same type. It also opens to perspectives in modeling, which we hope to address in the future. TROLL integrates several advances in plant physiology, but it also reflects the limits of this field. For example, plant respiration is less well understood than the photosynthesis cycle (Atkin et al. 2014). Allocation dynamic and mortality mechanisms are also less well known than assimilation (Malhi et al. 2015). TROLL could help test which process may be relevant for future improvements of DVMs, and also to propose empirical scaling-up relationships (Bellassen et al. 2010). Ecosystem experiments in tropical forests, such as the new generation of FACE experiments (Norby et al. 2016), throughfall exclusion experiments (Meir et al. 2015), nutrient addition experiments (Powers et al. 2015), and other in situ experimental approaches (Fayle et al. 2015) all provide great opportunities of data-model interactions and hypothesis testing on poorly known processes (Medlyn et al. 2015, 2016).

TROLL does not explicitly model the water cycle or plant hydraulics. The typical two-month dry season observed in French Guiana rarely results in major tree physiological stresses (Buchmann et al. 1997, Guan et al. 2015), and this explains the overall relatively good fit of the model with observations. However, this situation may change in the future and drought could then become a critical mechanism of tropical forest vulnerability (Boisier et al. 2015, Meir et al. 2015). It would thus be important to include the water cycle to project future ecosystem states. TROLL has an appropriate model structure to include a species-level description of drought tolerance, an important point since there is a strong inter-specific variation of plant drought tolerance (Engelbrecht and Kursar 2003, Martínez-Vilalta et al. 2014, Klein 2014, Maréchaux et al. 2015). Including the water cycle in the model would also help better represent the successional dynamics since temperature and VPD are higher in clearings than within dense canopy of mature tropical forest. This results in strong evaporative demand, and increased stomatal closure hence reduced carbon assimilation, which could explain why forest regeneration as simulated here was more rapid than empirical

observations (Marthews et al. 2008).

Carbon allocation was described empirically, assuming a fixed proportion of total NPP allocated to wood growth and foliage production, and through the use of fixed and field-derived allometric equations. This approach is similar to that developed in other forest growth models (eg. Fyllas et al., 2014; Köhler and Huth, 1998; Moorcroft et al., 2001). However, carbon allocation is a dynamic process that can vary with resource limitation, such as water and nutrients, and thus across sites (Litton et al. 2007, Chen et al. 2013, Doughty et al. 2014, Malhi et al. 2015a; Fig. 11). Rowland et al. (2014) demonstrated that the fitting of seasonal values of allocation parameters yields better match with empirical observations in a tropical forest. Scheiter and Higgins (2009) implemented an approach to ensure that the allocation to biomass pools depends on the most limiting resource (Friedlingstein et al. 1999), but a mechanistic understanding of plant carbon allocation is still lacking. One step forward would be to explicitly represent allocation of photosynthates to C reserves (non-structural carbohydrates, NSC; Dietze et al. 2014; Fig. 11). It would be useful to add a pool of NSC because mortality due to carbon starvation (see d_n in eq. 23) could then be expressed in terms of NSC depletion. Fortunately, the role of such dynamic NSC storage in plant metabolism maintenance, growth control and mortality processes is being increasingly studied (Sala et al. 2012, Körner 2015, Martínez-Vilalta et al. 2016).

More generally, closing the carbon cycle is an important challenge. Soil carbon fluxes, root exudates, and heterotrophic respiration are currently absent in TROLL, despite their known importance in carbon cycle (e.g. Bonal et al. 2008, Davidson et al. 2011). A proper comparison of the model against eddy-flux data would require closing the carbon balance (Baldocchi et al. 2001, Baldocchi 2003, Bonal et al. 2008). Adding these features would also be important to explore the role of mycorrhizal interactions in mediating nutrient uptake in plants, but also in better understanding species complementarity on ecosystem function. The integration of an explicit nutrient cycle with co-limitation for nitrogen and phosphorous would also be a very useful advance (Prentice et al. 2007, Fernández-Martínez et al. 2014, Powers et al. 2015; Fig. 11) given the on-going alteration of nutrient availability by humans (Peñuelas et al. 2013).

Herbivory makes a major contribution to carbon and nutrient cycles, as herbivores consume as much as ca. 20% of foliar production in tropical forests (Metcalfe et al. 2014) and because they regulate forest productivity (Terborgh et al. 2001). Attempts have already been made to explicitly model the interaction of plant dynamics and their predators (Harfoot et al. 2014), but our detailed model offers an opportunity to detail the host-specificity of predators,

and their individualistic response to environmental changes. For instance, it would be possible, using TROLL, to model the joint dynamics of plants and herbivorous insects (Forister et al. 2015). To that end, manipulative experiments on whole ecosystems would prove very valuable (Fayle et al. 2015).
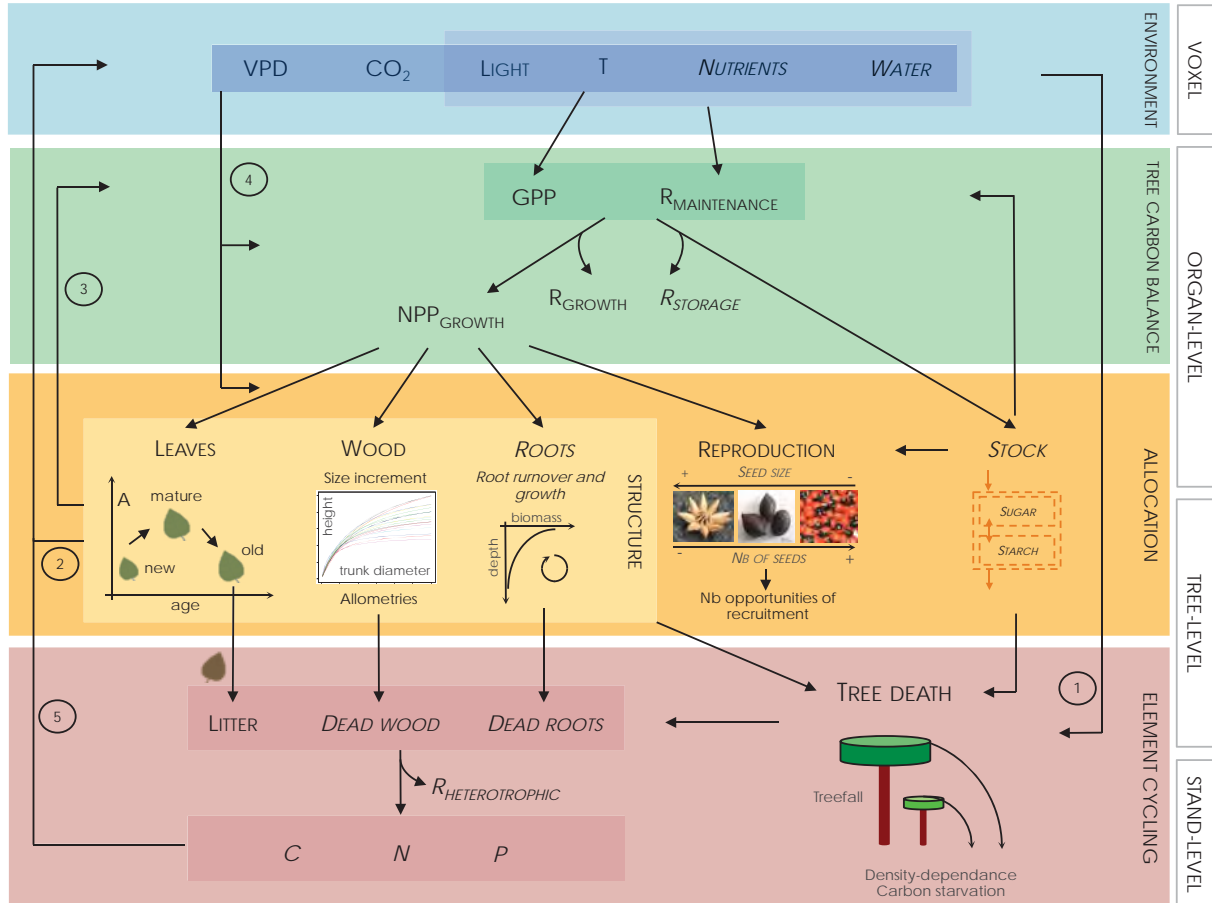
Fig. 11. Flow diagram for the TROLL model. Elements in italic letters refer to processes not included in this present version, but discussed in this study.

Modeling biodiversity in forest ecosystems

Tropical forests shelter thousands of co-occurring tree species (Hubbell et al. 2008) and these span a broad range of ecological and functional properties. Advances in plant functional trait research represent a major advance in understanding plant physiology and ecological functions (Kattge et al. 2011, Díaz et al. 2016). One original feature of TROLL is that it describes species individually, thus providing a finer description of biodiversity than the usual PFT-approaches. Importantly, simulation results were obtained using seven species-level parameters (Table 1), which are relatively easy to measure in the field: allometric parameters can be obtained from the observation of 10-20 individuals spanning the size range of the

species, and leaf- and stem-level parameters can be gained from a limited sampling of tissue (Patiño et al. 2012). Thus, the model requirements of TROLL parallels closely current efforts of trait data collection, and for this reason it should be applicable for many tropical forests sites.

In TROLL, species parameters are fixed and prescribed, and are identical among the individuals of the same species. Thus, we assume that species represent evolutionary stable traits associations and overlook intra-specific functional variability, which is a reasonable starting point. There is abundant evidence of the importance of the role of intra-specific variation for adaptation (Chesson 2000, Albert et al. 2011, Laughlin et al. 2012, Snell et al. 2014, Le Bec et al. 2015), and these processes may contribute to buffering the effect of climate change through new phenotypes better adapted to new conditions (e.g. Scheiter et al. 2013). The object-oriented code structure of TROLL is suited to the integration of such evolutionary processes, and this is an interesting avenue for future research. More generally, physiology- and individual-based, mechanistic and modular models such as TROLL constitute efficient tools to test alternative hypotheses on the understudied processes discussed above, explore alternative management scenarios, or experimental set-ups, as now discussed.

One driving motivation behind keeping a species-level description in the model is that each species has its peculiar evolutionary history and ecology, and should therefore considered as the most natural unit in the description of natural communities (Gleason 1926). Recent modeling studies have followed a different route to model biodiversity. They did not explicitly model species one by one, but they used empirically documented functional trade-offs (Wright et al., 2004) to constrain individual traits associations into a biologically realistic space (Scheiter et al. 2013, Sakschewski et al. 2015). This approach is computationally efficient and less data demanding than ours, and may prove fruitful in the future. However, it is predicated on varying trait combinations within strictly limited constrains, that may ignore a more complex set of constraints (Laughlin 2014, Li et al. 2015, Asner et al. 2016).

Also the integration of species identity in TROLL yields outputs that are most similar to field inventories. Correspondence between field data and model structure is desirable to take advantage of empirical knowledge and to validate models. But it has also important practical implications. Indeed, about half of standing tropical forests are designated for timber production (Blaser et al. 2011), and it is important to assess and predict the impact of logging scenarios on carbon losses and biodiversity and structure modifications. Species-level integration could inform management approaches, as logging practice crucially depends on

commercial species of particular interest. For example, in French Guiana, only two species, *Dicorynia guianensis* and *Qualea rosea* account for up to 60% of the total timber production. TROLL could thus help assess forest vulnerability to timber exploitation (eg. Fargeon et al., 2016) by modeling logging scenarios, selecting focal species at a reference diameter.

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Appendix 1

In this Appendix, we detail how the half-hourly microclimatic environment is deduced from empirical data. We first prescribe the monthly average of the daily maximum incident photosynthetic PPFD ($PPFD_{top,max,month}$). This single value per month describes the seasonality in light intensity. We also define monthly average of the daily maximal T ($T_{top,max,month}$) and of the VPD ($VPD_{top,max,month}$), as measured above the canopy. Finally the monthly average mean nighttime T ($T_{night,month}$) is assumed constant throughout the night and within the canopy. The input field for these four variables is a matrix of 12x4 values that are easily computed from standard meteorological stations.

Attenuation of PPFD within the canopy is modeled using a local Beer-Lambert extinction law:

$$PPFD_{max,month}(v) = PPFD_{top,max,month} \times \exp[-k \times LAI(v)] \tag{A1}$$

with k the light extinction rate k. Temperature and VPD also decrease within forest canopies. To model this gradient we define the variable $\lambda = LAI(v)/LAI_{sat}$ with LAI_{sat} a threshold LAI. The regime $\lambda < 1$ defines a boundary layer (top voxels). In this part of the canopy, T and VPD vary as follows:

$$T_{max,month}(v) = T_{top,max,month} - \Delta T \times \lambda \tag{A2a}$$

$$VPD_{max,month}(v) = VPD_{top,max,month} \times \left[C_{VPD0} + (1 - C_{VPD0}) \sqrt{(1-\lambda)} \right] \tag{A3a}$$

where ΔT and C_{VPD0} are set parameters. In the understory ($\lambda \geq 1$), we assume that both T and VPD are constant:

$$T_{max,month}(v) = T_{top,max,month} - \Delta T \tag{A2b}$$

$$VPD_{max,month}(v) = VPD_{top,max,month} \times C_{VPD0} \tag{A3b}$$

In tropical forests, understory air relative humidity reaches 100%. This implies that ground-level temperature (defined by eq. A2b) is close to the dew point temperature, and that VPD is close to zero. However, departure from these values is expected during at least a few days every month. The set of equations 2-3 is in qualitative agreement with empirical observations of microclimate gradients within canopy (Shuttleworth 1985, Shuttleworth et al. 1989, Camargo and Kapos 1995). Model dynamics depended little on the values of ΔT, C_{VPD0} and LAI_{sat} in realistic ranges (results not shown).

We also need to model how microclimate varies within a typical day. Half-hourly variation during daylight of above-canopy PPFD, T and VPD were prescribed. We generated

half-hourly trajectories of the mean daily course of light intensity (p_t), temperature (t_t), and VPD (v_t), so that the maximum value of the functions was set to 1. The input data was then a 48x3 matrix of half-hourly data. Half-hourly environmental variables for an average day for each month were computed for each voxel as follows:

$$PPFD_{month}(v,t) = p_t \times PPFD_{max,month}(v)$$
$$T_{month}(v,t) = t_t \times T_{max,month}(v)$$
$$VPD_{month}(v,t) = v_t \times VPD_{max,month}(v) \qquad (A4)$$

Equations 2-4 yield mean half-hourly microclimatic data as an input for the model.

Appendix 2

In this Appendix, we provide explicitly the temperature dependencies used in the phostosynthesis model.

V_{cmax} and J_{max} vary with temperature as in Bernacchi et al. (2003):

$$V_{cmax}(T) = V_{cmax}(25°C) \times e^{(26.35-65.33/(R\times(T+273.15)))}$$

$$J_{max}(T) = J_{max}(25°C) \times e^{(17.57-43.54/(R\times(T+273.15)))}$$

Γ^* and K_m were expressed as in von Caemmerer (2000):

$$\Gamma^*(T) = 37 \times e^{23.4\times(25-T)/(298\times R\times(273+T))}$$

$$K_m(T) = 404 \times e^{59.36\times(25-T)/(298\times R\times(273+T))} \times (1 + 210/(248 \times e^{35.94\times\frac{25-T}{298\times R\times(273+T)}}))$$

R is the molar gas constant (8.314 kJ K^{-1} mol^{-1}), and T is the temperature in degree Celsius.

Appendix 3
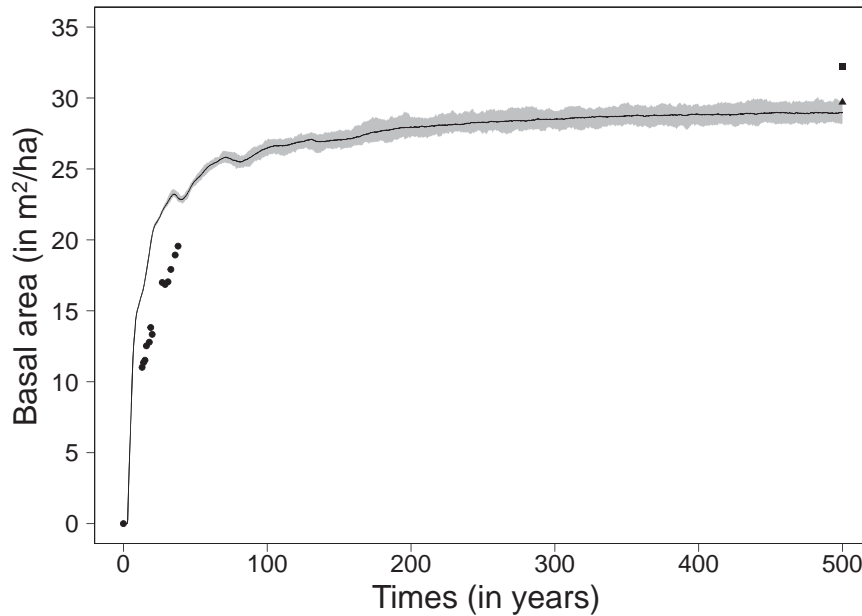
Fig. A1. Changes of total basal area (trees with dbh $\geq$ 10 cm, in m^2/ha), during a 500-year-long forest regeneration, starting from bare soil, with a monthly timestep and a constant external seed rain. The solid black line corresponds to the median while the shaded grey area represents the range across 100 simulations. Circle symbols correspond to the observed early-regeneration values, square and triangle symbols to the Paracou and Nouragues mature forest values, respectively.
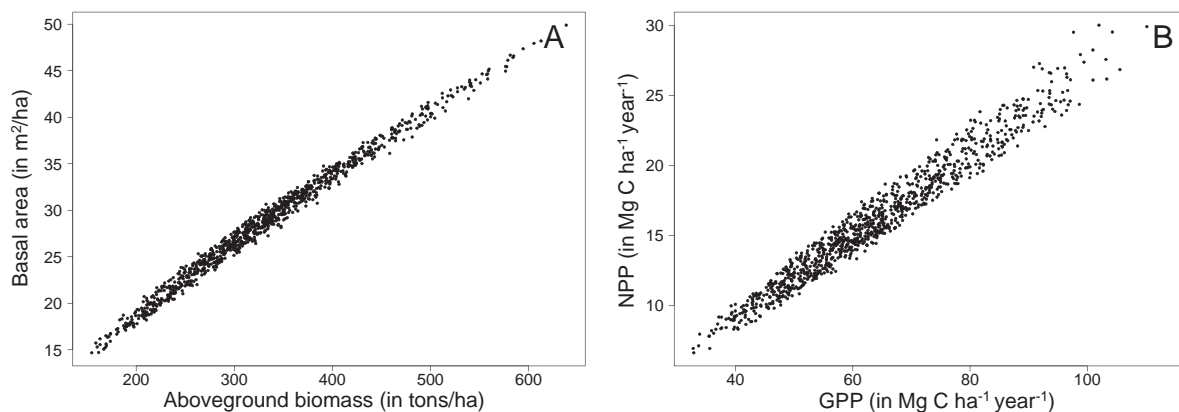
Fig. A2. Covariation of (A) aboveground biomass (AGB) and basal area; and (B) gross primary productivity (GPP) and net primary productivity (NPP), as revealed by a sensitivity analysis (1000 independent simulations) varying six parameter values (ϕ, k, f$_{wood}$, f$_{canopy}$, m and g$_1$) randomly and independently (Table 2). Each point corresponds to one 500-year simulation (with monthly timestep), and outputs were averaged over the 20 last iterations.

As aboveground biomass and basal area on one hand, and GPP and NPP on the other hand were tightly correlated (R^2=0.99 and 0.96 respectively), only AGB and GPP were discussed in the main text.

Appendix 4
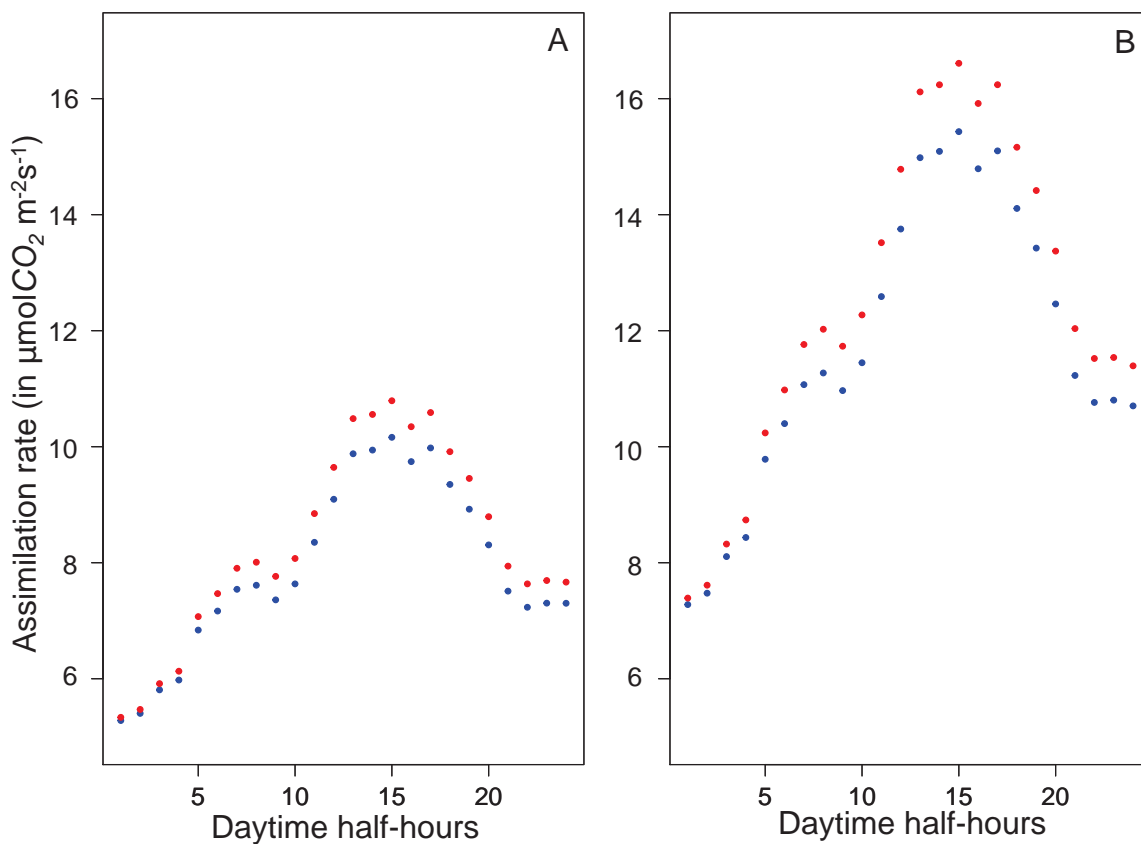
Fig. A3. Daily variation of the Rubisco-limited assimilation rate in full sunlight (A_v in eq. 3), as computed in TROLL, for (a) the coldest and wettest month of the year ($T_{top,max,month}$=28.5°C, $VPD_{top,max,month}$=1.07 kPa) and (b) the hottest and driest month of the year ($T_{top,max,month}$=33.1°C, $VPD_{top,max,month}$=2.47kPa), with both g_1=2 (blue) and g_1=5 (red). V_{cmax} value at T=25°C was computed for *Dicorynia guianensis* (V_{cmax}=39.7 $\mu molCO_2$ m^{-2}s^{-1}).

The conditions under which the plots are drawn are conservative since corresponding to the conditions were changes in VPD and temperature are the highest, and thus influence of g_1 should be the strongest.

Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest

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Chapter outline

Considering the lack of both knowledge and data informing tropical tree species responses to drought, hydraulic responses were not explicitly represented in the model described and used in **Chapter 1**. However predicted increase in drought intensity and frequency may impact forest structure and composition, and their vulnerability has already been observed in natural and artificial experiments. This **Chapter 2** aims at investigating the drought tolerance diversity within an Amazonian forest community, as revealed by the leaf water potential at turgor loss point (π_{tlp}). This work benefits from the recent development of a standardized method much more rapid than the commonly used time-consuming pressure-volume curve method. It thus allows to consider measuring π_{tlp} at the community level. Using this method, the first community-level assessment of the diversity of such a *hard* drought-tolerance trait in an Amazonian rainforest is presented, spanning 165 trees of 71 species, at three sites within forests in French Guiana.

Abstract

Amazonian droughts are predicted to become increasingly frequent and intense, and the vulnerability of Amazonian trees has become increasingly documented. However, little is known about the physiological mechanisms and the diversity of drought tolerance of tropical trees due to the lack of quantitative measurements.

Leaf water potential at wilting or turgor loss point (π_{tlp}) is a determinant of the tolerance of leaves to drought stress, and contributes to plant-level physiological drought tolerance. Recently, it has been demonstrated that leaf osmotic water potential at full hydration (π_0) is tightly correlated with π_{tlp}. Estimating π_{tlp} from osmometer measurements of π_0 is much faster than the standard pressure-volume curve approach of π_{tlp} determination. We used this technique to estimate π_{tlp} for 165 trees of 71 species, at three sites within forests in French Guiana. Our dataset represents a significant increase in available data for this trait for tropical tree species.

Tropical trees showed a wider range of drought tolerance than previously found in the literature, π_{tlp} ranging from -1.4 to -3.2 MPa. This range likely corresponds in part to adaptation and acclimation to occasionally extreme droughts during the dry season. Leaf-level drought tolerance varied across species, in agreement with the available published observations of species variation in drought-induced mortality. On average, species with a more negative π_{tlp} (i.e., with greater leaf-level drought tolerance) occurred less frequently across the region than drought-sensitive species.

Across individuals, π_{tlp} correlated positively but weakly with leaf toughness (R^2=0.22, P=0.04) and leaf thickness (R^2=0.03, P=0.03). No correlation was detected with other functional traits (leaf mass per area, leaf area, nitrogen or carbon concentrations, carbon isotope ratio, sapwood density or bark thickness).

The variability in π_{tlp} among species indicates a potential for highly diverse species responses to drought within given forest communities. Given the weak correlations between π_{tlp} and traditionally measured plant functional traits, vegetation models seeking to predict forest response to drought should integrate improved quantification of comparative drought tolerance among tree species.

Key-words: climate change, French Guiana, functional traits, plant water relations, tropical trees, wilting

Introduction

Amazonian forests play a fundamental role in global biogeochemical cycles (Malhi *et al.* 2008; Boyce *et al.* 2010; Saatchi *et al.* 2011; Harper *et al.* 2013). However, these forests have been predicted to be vulnerable to drought intensification in simulations coupling a global climate model and a dynamic global vegetation model (Cox *et al.* 2000; Huntingford *et al.* 2008). This critically discussed "Amazonian dieback" scenario predicts significant increases in mortality rates for Amazonian trees, leading to a catastrophic transition into a savannah-type vegetation (Malhi *et al.* 2009; Good *et al.* 2013; Huntingford *et al.* 2013). The observed increase in Amazonian tree mortality during the 2005 and 2010 droughts illustrated this vulnerability (Phillips *et al.* 2009; Lewis *et al.* 2011; Saatchi *et al.* 2013; Hilker *et al.* 2014), and such droughts may increase in frequency and intensity in the future (Malhi *et al.* 2008; Lewis *et al.* 2011; Joetzjer *et al.* 2013).

Through-fall exclusion experiments in Amazonia confirmed that an increased drought intensity resulted in reduced tree growth and increased tree mortality, leading in turn to a net carbon release of the ecosystem (Nepstad *et al.* 2002; Fisher *et al.* 2007; Brando *et al.* 2008). These experiments also revealed species differences in tree vulnerability, with some but not all species presenting increased mortality rates due to water stress (Nepstad *et al.* 2007; da Costa *et al.* 2010). Previous studies also found strong species differences in physiological drought tolerance among selected species within a given vegetation type (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008; Kursar *et al.* 2009; Blackman, Brodribb & Jordan 2012; McDowell *et al.* 2013). Drought may thus strongly shape tropical tree species distributions through species-specific effects on growth and mortality (Engelbrecht *et al.* 2007; Jabot & Chave 2011). However, the diversity of species responses to drought has been poorly accounted for in vegetation models (Sitch *et al.* 2008; Powell *et al.* 2013; Xu *et al.* 2013). Improving the representation of drought responses across species-rich tropical tree communities therefore remains a critical research objective. This study aimed to document the drought tolerance of Amazonian trees, with a special focus on variation among species, by implementing a novel method for rapidly measuring leaf-level drought tolerance.

One well-established approach to study the drought tolerance of plants is to quantify their physiological responses to water supply at the seedling stage using reciprocal transplant experiments (Cao 2000; Engelbrecht *et al.* 2007; Kursar *et al.* 2009; Urli *et al.* 2013).

Although this approach has yielded insightful findings, it is applicable to a limited number of species, and only at the seedling stage. It cannot be readily applied to canopy trees that account for most of the biomass of the ecosystem and that have been found to be particularly vulnerable to water stress in several studies (Nepstad *et al.* 2007; da Costa *et al.* 2010). A different route consists of measuring plant functional traits for many species, especially for use in vegetation models (Fyllas, Quesada & Lloyd 2012). The search for traits that may be used as proxies of plant tolerance to drought has generated an important literature (Niinemets 2001; Hacke *et al.* 2001; Lamont, Groom & Cowling 2002). However, the use of structural traits – in particular leaf mass per area (LMA), leaf thickness, leaf toughness, and wood density – as a proxy for drought tolerance remains controversial (Zanne *et al.* 2010; Bartlett, Scoffoni & Sack 2012b; Fortunel *et al.* 2014). Thus physiological traits with strong mechanistic links with plant responses to water stress are needed to explore drought tolerance patterns in tropical forests. These traits would also facilitate exploring the relationship between drought tolerance and rarity in tropical forest trees and therefore improve understanding of the drivers of tropical forest diversity and composition.

In a recent review, Bartlett, Scoffoni & Sack (2012b) argued that leaf water potential at wilting (or turgor loss point, henceforth denoted π_{tlp}), strongly underlies ecological drought tolerance and species distributions relative to water supply within and across biomes (see also Lenz, Wright & Westoby 2006). This plant functional trait represents the leaf water potential that induces wilting. Thus, leaves with a more negative π_{tlp} (measured in MPa) remain turgid at more negative water potentials, and tend to maintain critical processes, such as leaf hydraulic conductance, stomatal conductance, and photosynthetic gas exchange, under drier conditions (Cheung, Tyree & Dainty 1975; Abrams, Kubiske & Steiner 1990; Brodribb *et al.* 2003; Bartlett *et al.* 2012b; Guyot, Scoffoni & Sack 2012). Thus a more negative value for π_{tlp} contributes to greater leaf-level and therefore also plant-level drought tolerance.

Previously, π_{tlp} has been estimated from pressure-volume curves, which measure the decline of leaf water potential as the leaf dehydrates. This standard method of π_{tlp} determination is time-consuming and impractical for the hundreds of species occurring in most tropical forests (Koide *et al.* 1989). However, another pressure-volume curve trait, the leaf osmotic potential at full hydration (π_o), was repeatedly found to be an excellent correlate for π_{tlp} (Sack *et al.* 2003; Lenz *et al.* 2006; Blackman, Brodribb & Jordan 2010; Scoffoni *et al.* 2011; Bartlett *et al.* 2012b). Based on the above correlation, and finding its basis in the fundamental equations describing leaf physiology, Bartlett *et al.* (2012a) inferred modelled

values of π_{tlp} from osmometer measurements of π_o. The $\pi_o - \pi_{tlp}$ relationship was calibrated using diverse species, including tropical rainforest species. This method has the advantage of being much faster than the standard pressure-volume curve approach.

Here we used this method to gather new π_{tlp} data for 71 woody plant species in French Guiana, and to compare these data with previously published data for species of other tropical forests. We used this new dataset to test hypotheses for the diversity of tropical forest tree drought tolerance, as estimated by the π_{tlp}, its relationships with species rarity, its variability with local environmental conditions, and its potential coordination with other functional traits. We hypothesized that (1) because drought tolerance arising from adaptation and/or acclimation incurs a significant cost, species with high drought tolerance would be relatively infrequent in moist tropical forests and thus π_{tlp} would correlate negatively with species rarity; (2) π_{tlp} depends on local environmental conditions, and thus, individuals growing in soils with a lower water retention capacity are more drought-tolerant; and (3) π_{tlp} would be correlated, even if weakly, with other functional traits previously hypothesized to be associated with drought tolerance or lower water availability, such as higher leaf mass per area and wood density.

Materials and methods

Study sites and sampling strategy

Field measurements were conducted at three plots within two moist tropical forests in French Guiana. The Nouragues Ecological Research Station is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05' N, 52°40' W; Bongers *et al.* 2001). The bedrock is varied at this site: the majority of the forest grows on metamorphic bedrock of the Paramaca series, covered with clay soil, while a smaller area surrounding the granitic outcrop has granitic and crystalline bedrocks covered with soil with a mixture of clay and sand derived from the bedrock (Grimaldi & Riéra 2001). Data were collected in two 1-ha permanent plots, one on clay soil (NL11 on Grand Plateau, hereafter referred to as the "clay site"), and the other on clay-sand soil (NH20 on Petit Plateau, hereafter referred to as the "clay-sand site"). The Paracou Research Station is located close to

the village of Sinnamary and 20 km from the coast (5°15' N, 52°55' W; Gourlet-Fleury, Guehl & Laroussinie 2004). The bedrock is a metamorphic formation of the Precambrian Shield, dominated by schists and sandstones. Soils are limited in depth by a lateritic pan, which has a low permeability and leads to lateral drainage during heavy rains (Ferry *et al.* 2010). At Paracou, we collected data from one 1-ha plot (P006, hereafter referred to as the "sandstone site"). Having different textures, soils at the three sites are expected to present contrasting water holding capacities, with clay-sand and sandstone sites being more drained than the clay site. All three sites receive c.a. 3000 mm/yr rainfall, with significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. A long wet season lasts from December to July, often interrupted by a short dry period in March. The dry season lasts from the end of August to November with 2-3 months with precipitation < 100 mm/mo.

In 2007 and 2008, the three 1-ha plots were fully censused for trees ≥ 10 cm diameter at breast height (DBH) (Baraloto *et al.* 2010a), and species richness ranged between 150 and 200 species per hectare. During that initial sampling phase, all trees (with DBH ≥ 10 cm) in each plot were sampled for many leaf and stem functional traits, including toughness (estimated by punch tests, using a penetrometer), carbon and nitrogen concentrations, carbon isotope ratio (δ^{13}C), and sapwood density and bark thickness (methods used in the determination of these traits are described in Baraloto *et al.* 2010a).

Measurements of leaf drought tolerance traits were conducted in September 2012 at the peak of the dry season. The trees were selected so that the most locally-abundant species were represented in our sampling, to ensure that at least two individuals per species were collected per plot, and to maximize species-level variation in wood density, which has often been associated with drought tolerance (Hacke *et al.* 2001; Santiago *et al.* 2004; Chave *et al.* 2009; Markesteijn *et al.* 2011a; b). Small branches were collected by climbing the trees using the French-spike method (Fonderies Lacoste, Excideuil, France; De Castilho *et al.* 2006) or directly from the ground using a clipping pole. When climbing the selected trees, we also occasionally sampled neighbouring trees, which explains why a few species were sampled only once in the final dataset. In total, we collected leaves for 165 trees (48, 63 and 54 from the clay, clay-sand site, and sandstone sites, respectively), from 71 species (33, 40 and 19 species from the clay, clay-sand and sandstone sites, respectively), representing 29 families (nomenclature follows the Plant List http://www.theplantlist.org/).

Measurements of leaf thickness, leaf area, leaf dry mass and leaf mass per area (LMA) were conducted on the same leaves as for leaf drought tolerance traits in September 2012. Leaf thickness was computed as the mean of thickness measurements at the bottom, middle and top of the leaf, measured on the fresh leaves using digital calipers (Mitutoyo, Japan). Thick woody petioles were removed and fresh leaves were scanned using a portable scanner (Canon LiDE 60, Canon USA, Lake Success, NY, USA). Leaf area was measured manually from the scans using the ImageJ software (http://imagej.nih.gov/ij/). Leaves were then oven-dried at 65°C for 48 h and weighted for estimating leaf dry mass and computing LMA (leaf dry mass divided per leaf area).

Measurement of π_{tlp} values

We assessed the leaf turgor loss point, π_{tlp}, from a previously established linear relationship with the osmotic potential at full hydration (π_o), in turn directly measured with a vapour pressure osmometer (Vapro 5520, Wescor, Logan, UT) (Bartlett *et al.* 2012a).

Branches were collected from the selected trees and placed in opaque bags with wet paper towel, then recut under water at least two nodes distal to the original cut and allowed to rehydrate overnight covered with plastic, and branch ends underwater. Three mature leaves were collected from each rehydrated branch and stored in Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA) with a wet paper towel. One disc was sampled from each leaf centrally between the midrib and margin with an 8-mm-diameter cork borer, avoiding first- and second-order veins. The discs were wrapped in foil and frozen by immersion in liquid nitrogen (LN_2) for at least 2 minutes, then immediately punctured 10-15 times with sharp-tipped forceps and sealed in the osmometer chamber, using the standard 10 µL chamber well. The discs were exposed to air for less than 40 seconds for all steps between removing the leaf from the Whirl-Pak bag and sealing the disc in the osmometer. The equilibrium solute concentration value c_0 (in mmol kg^{-1}) was recorded from the osmometer when the difference between consecutive 2-minute measurements fell below 5 mmol kg^{-1}. This value was converted to π_o values from the osmometer (π_{osm}) using the van't Hoff equation relating solute concentration to vapour pressure:

$$\pi_{osm} = -\frac{2.5}{1000} \times c_0 \qquad (1)$$

where the numerator of the first term represents R×T = 2.5 L MPa mol^{-1} at 25°C, with R the ideal gas constant and T the temperature in degrees Kelvin.

The value of π_{tlp} was estimated from π_{osm} using the previously published regression equation relating π_{osm} to pressure-volume curve turgor loss point values, developed from 30 woody species representing a wide range of leaf structural features and habitat preferences (n=30 species, R^2=86%, p<2.10^{-12}, π_{osm} range=[-3.03, -0.64] MPa and π_{tlp} range=[-3.00, -1.02] MPa ; Bartlett *et al.* 2012a):

$$\pi_{tlp} = 0.832 \times \pi_{osm} - 0.631 \qquad (2)$$

This correlation was established using osmometer π_o values (π_{osm}) and π_{tlp} values measured with the standard but very time-consuming pressure-volume curve method, for 15 diverse species sampled in gardens adjacent to the University of California, Los Angeles campus, originating from a range of vegetation zones from chaparral to tropical wet forest, and 15 species growing in natural conditions in Chinese tropical rainforest (Bartlett *et al.* 2012a). The fit of Equation (2) was not significantly different for these two subgroups, consistent with expectations from theory that this estimation of turgor loss point is independent of leaf structure and habitat preference and can be applied to species across vegetation zones (Bartlett *et al.* 2012a). The π_{osm} range of the correlation dataset encompassed the full range of the π_{osm} values measured in this study (π_{osm} range=[-3.02, -0.94] MPa). When this correlation dataset was restricted to the tropical rainforest species group only, the π_{osm} range (π_{osm} range=[-1.70, -0.70] MPa; Bartlett *et al.* 2012a) encompassed 86% of the range of our measured π_{osm} values. All π_{osm} and π_{tlp} data are available (see Appendix S1 in Supporting Information).

Data analysis

We compared the π_{tlp} values for the measured trees with a published compilation of π_{tlp} values for moist tropical forests measured during the wet season (n=50 for moist tropical forests, data available in the Supplementary material of Bartlett *et al.* 2012b). We tested for species differences in π_{tlp} for a subset of 13 species for which at least 5 individuals were sampled (n=82 individuals). We also tested for species differences in π_{tlp} within two well-sampled families (with at least 4 sampled species for which at least 5 individuals were sampled; Fabaceae, n=4 species and 26 individuals; Lecythidaceae, n=4 species and 25 individuals). We used linear models (ANOVA), with species as a fixed effect, and tested for pairwise species differences with Tukey tests. The relative contribution of within- and across-species differences to π_{tlp} variability was quantified with variance partitioning (Sokal & Rohlf 1987).

To test the significance of the variation of π_{tlp} values among study sites, we used linear models (ANOVA), with site treated as a fixed effect. Tukey tests were used to determine which pairwise comparisons were significantly different.

We also investigated the relationship between species mean π_{tlp} and regional occupancy, estimated as the number of occurrences across 478 $0.25° \times 0.25°$ grid cells within the Guiana Shield (Mouillot *et al.* 2013). Regional occupancy measures one dimension of species rarity, not necessarily correlated with local abundance. We conducted a Spearman rank-order correlation test (r_s) between species-averaged π_{tlp} and regional occupancy.

We tested correlations between π_{tlp} and leaf-level plant functional traits measured on the same leaves (area, thickness and mass per area) at the individual level. We also tested the correlation between species-averaged π_{tlp} and previously measured species-averaged leaf-level and stem-level plant functional traits (toughness, carbon and nitrogen concentrations, $\delta^{13}C$, sapwood density and bark thickness). The latter traits were measured five years earlier (in 2007; Baraloto *et al.* 2010a) and not on the same leaves for each individual. Hence, we tested these correlations for species means to minimize the effect of temporal and intra-canopy variability within individuals. For this second set of analyses, we included only species for which trait values had been measured for at least 3 individuals for both π_{tlp} and the tested trait (n ranged from 14 to 19 species).

All statistical analyses were conducted using the R software (version 3.0.2; R Core Team 2013).

Results

Variation in mean π_{tlp} across species

The π_{tlp} varied strongly across species (Fig. 1; ANOVA, $P<1.10^{-6}$), with 40% of the variance in π_{tlp} associated with species differences (n=13 species and 82 individuals). Strong species differences were exemplified by *Dicorynia guianensis* (Fabaceae) and *Eschweilera coriacea* (Lecythidaceae), which had less negative π_{tlp} values than the average (-1.71 ± 0.16 MPa and -1.83 ± 0.06 MPa, respectively) and *Lecythis poiteaui* (Lecythidaceae), which had a more negative π_{tlp} than average (-2.58 ± 0.16 MPa). *Protium* (Burseraceae) individuals also had

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significantly more negative π_{tlp} than average (-2.28 ± 0.06 MPa; t-test, P=0.003). Species differences explained 31% and 68% of the variability within our subset of Fabaceae and Lecythidaceae respectively (n=4 species for both families and 25-26 individuals; ANOVA, P=0.02 and P<1.10^{-5} respectively).
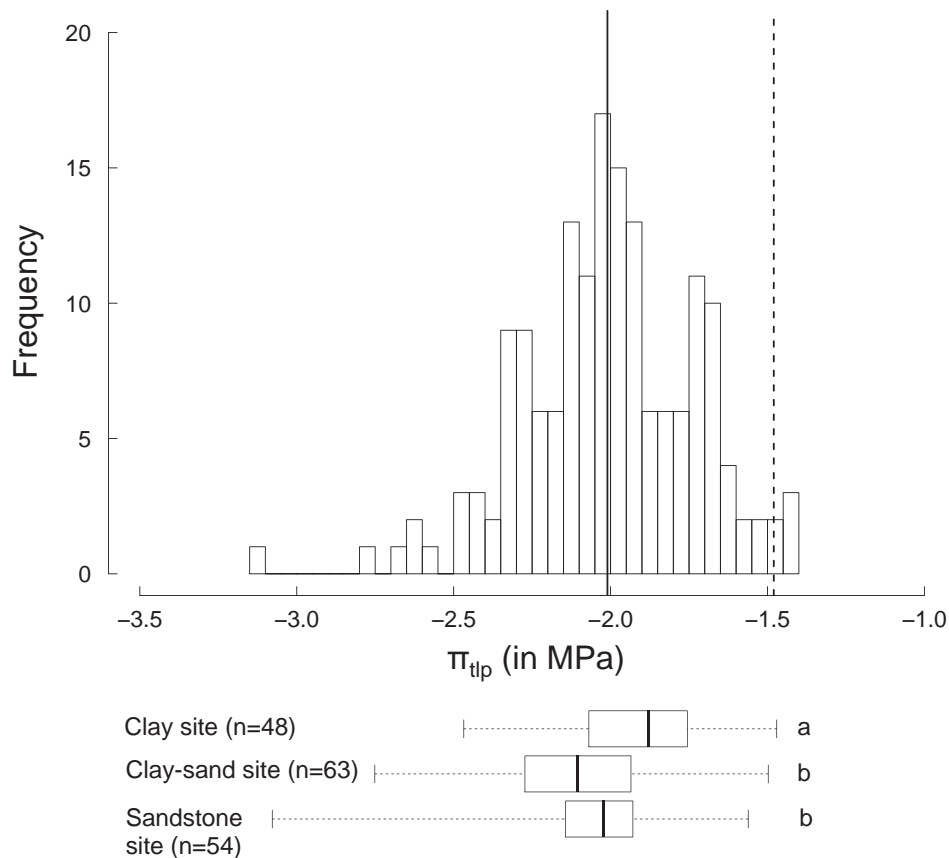
Fig. 1. Diversity of leaf drought tolerance across 71 species in a tropical forest. Upper panel: histogram of leaf-level water potential at turgor loss point (π_{tlp}, in MPa) in our dataset (n=165 individuals). Solid and dashed lines indicate mean of π_{tlp} values in our dataset and in Bartlett *et al.* (2012b) dataset, respectively. Lower panel: boxplots for the three study plots in French Guiana (with 33, 40 and 19 species from the clay, clay-sand and sandstone sites, respectively, and 6 species sampled in the three sites). Different lower case letters indicate a significant difference between sites π_{tlp} means (Tukey test: P<0.05).

Drought-tolerant species are regionally less frequent than drought-intolerant ones

Species with a more negative π_{tlp} tended to have a lower regional occupancy (Fig. 2; Spearman rank-order correlation $r_s = 0.68$; P=0.01). In particular, the most frequent species, *Eschweilera coriacea,* which occurred at 62/478 grid cells across Amazonia, had a less

negative π_{tlp} than average (t-test, P=0.03). Conversely, the most drought-tolerant species, in terms of its π_{tlp}, *Lecythis poiteaui,* is regionally infrequent, occurring at 26/478 grid cells.
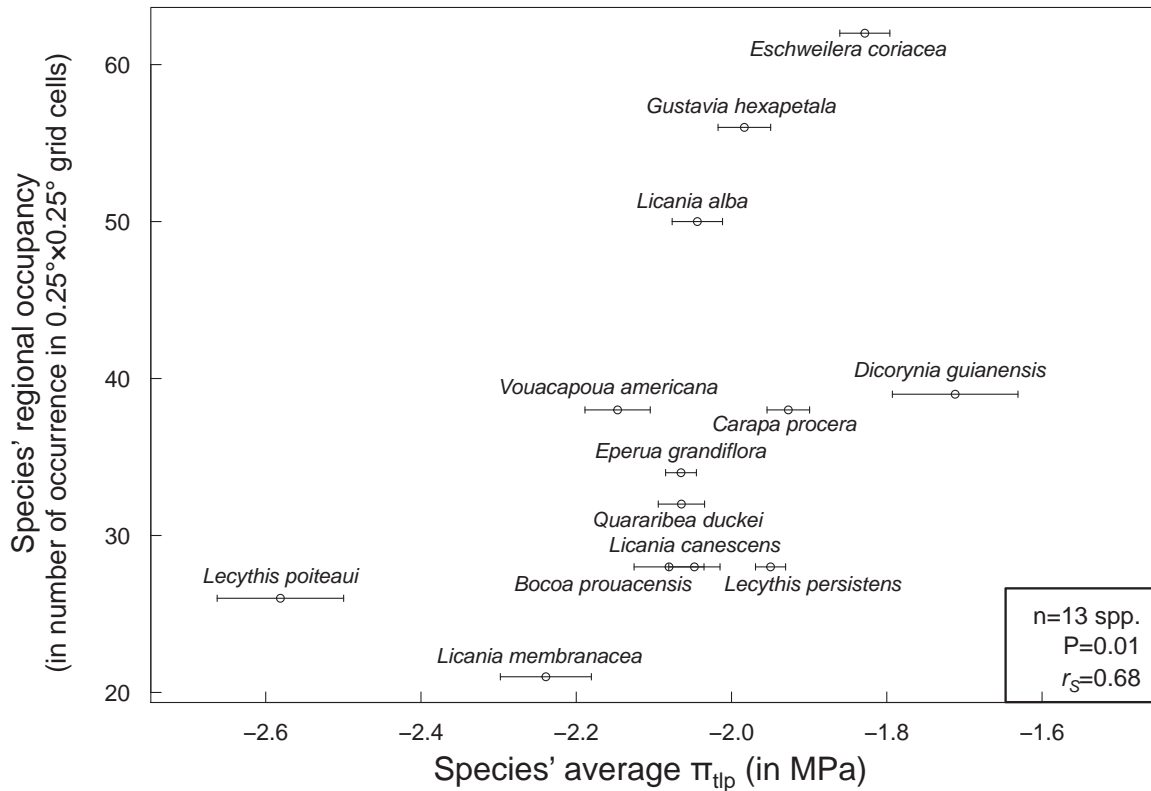
Fig. 2. Relationship between species regional occupancy and species' average leaf turgor loss points (π_{tlp}, in MPa), for species for which we sampled at least five individuals. Regional occupancies were estimated as the number of occurrences in 478 0.25°×0.25° grid cells within the Guiana Shield. Whisker plots indicate standard errors of the mean.

Wider range of π_{tlp} than previously accounted for in moist tropical forests

The mean π_{tlp} (±SE) across species in the study plots was -2.01 ± 0.02 MPa. This mean value was substantially more negative than that determined from data previously compiled for moist tropical forests during the wet season (Table 1; Fig. 1; Bartlett *et al.* 2012b; t-test, P<0.005). The most negative values we measured were below the most negative value reported for this ecosystem compilation (Table 1; Bartlett *et al.* 2012b).

Table 1. Mean and standard error (SE) and range of π_{tlp} values at the three sites, and comparison with literature values.

Site	Number of individuals	Mean ± SE (MPa)	Min (MPa)	Max (MPa)
sandstone site	54	-2.03 ± 0.04	-3.15	-1.51
clay-sand site	63	-2.09 ± 0.04	-2.80	-1.44
clay site	48	-1.89 ± 0.03	-2.49	-1.41
Total	165	-2.01 ± 0.02	-3.15	-1.41
Bartlett *et al.* (2012b) data*	50	-1.48 ± 0.06	-2.56	-0.43

*Data for trees of moist tropical forests during the wet season from Bartlett *et al.* (2012b).

Variation in mean π_{tlp} across forest plots

The π_{tlp} varied significantly across our three sites (ANOVA, P < 0.005; Fig. 1). The mean π_{tlp} at the clay-sand site was similar to that for the sandstone site (Table 1; Tukey test, P=0.54), which is also on a well-drained soil with a large sandy fraction, ca. 100 km away, and both were on average marginally more negative than that of the clay site (Table 1; Fig. 1; Tukey tests, P<0.001 and P=0.02 for comparisons with the clay-sand and sandstone sites, respectively).

Weak correlation of π_{tlp} with other functional traits

Across species, a more negative π_{tlp} was associated with lower leaf toughness (Fig. S1a; P=0.04, R^2=22%, n=19 species). Additionally, a more negative π_{tlp} was weakly associated with lower leaf thickness (Fig. S1c; P=0.03, R^2=3%, n=151 individuals). We found no statistical association of π_{tlp} with other functional traits, i.e., leaf area, dry mass, dry mass per area (LMA; Fig. S1d), carbon and nitrogen concentrations per leaf mass, carbon isotope ratio (d^{13}C), sapwood density (Fig. S1b) or bark thickness.

Discussion

Leaf potential at turgor loss point primarily depends on species identity

We found strong variation in π_{tlp} among the tree species sampled in our study. Species identity was the best explanatory factor for the variation in leaf drought tolerance of trees and explained a major part of intra-family variability. Within the Lecythidaceae, *Eschweilera coriacea* had a higher (less negative) π_{tlp} than the all-species average, whereas *Lecythis poiteaui* had a more negative π_{tlp} than average. Similarly, within the Fabaceae, *Dicorynia guianensis* and *Vouacapoua americana* had π_{tlp} values that were substantially less and more negative respectively than the all-species average. Such a substantial variation in a key hydraulic trait has already been observed in another lineage (stem hydraulic vulnerability for species of *Cordia*; Choat, Sack & Holbrook 2007). However, despite such variation observed within lineages, our results are also remarkably consistent with observations of differences across genera in drought vulnerability in the long-term through-fall exclusion experiments conducted in the Brazilian Amazon (Caxiuanã, da Costa *et al.* 2010; Tapajós, Nepstad *et al.* 2007). In these experiments, some genera displayed much higher mortality than average under the drought treatment, especially the genus *Eschweilera*, which includes *Eschweilera coriacea*. In contrast, individuals belonging to genus *Protium* appeared relatively insensitive to the experimental drought. *Protium* also tends to increase in abundance in more seasonally dry forests across Amazonia (ter Steege *et al.* 2006). Consistent with these observations, *Protium* individuals included in our study had higher leaf-level drought-tolerance (lower-than-average π_{tlp}).

The above considerations suggest that π_{tlp}, measured at leaf level, is a useful integrative trait for plant-level tolerance. The π_{tlp} is a predictor of the leaf water status at which plant gas exchange declines during drought for many species, and its incorporation into photosynthetic models may allow for mechanistic predictions of the impacts of water stress on plant performance (Prentice et al. 2014). The ability to rapidly measure π_{tlp} therefore constitutes a significant step towards a better integration of tree responses to drought into vegetation models (Fisher *et al.* 2006; Smith *et al.* 2014). Future work is needed to determine for more species the correspondence of π_{tlp} with the responses of stomatal and hydraulic

conductances to soil drying, and its mechanisms (Meinzer *et al.* 1990; Williams & Ehleringer 2000; Brodribb *et al.* 2003; Fisher *et al.* 2006; West *et al.* 2012).

The influence of soil parameters on both species composition and drought tolerance is a crucial question for vegetation modelling in Amazonia (Sabatier *et al.* 1997; Kursar, Engelbrecht & Tyree 2005; Quesada *et al.* 2009; Condit *et al.* 2013). We found that trees at the clay site were less drought-tolerant than trees at the two other sites in our dataset, despite similar rainfall. This pattern may result from both differences in π_{tlp} within species across environmental variation (i.e., plasticity and ecotypic variation), and/or from site differences in species composition. Indeed, even though the clay and clay-sand sites are only a few hundred meters apart, they harbour distinct tree floras, and this potential environmental filtering may be in part due to differential soil water retention ability (see also Lenz *et al.* 2006). A more exhaustive sampling across the local flora would help determine the relative extent to which site conditions, community composition and intra-species plasticity contribute to differences in π_{tlp} across geographic and environmental gradients.

Drought tolerance as predicted by π_{tlp} showed a positive trend with regional occupancy across our well-sampled species (Fig. 2). Based on this observation, we infer that drought-sensitive canopy trees are more widely distributed in the rain forests of the Guiana Shield compared to more drought-tolerant trees. If confirmed, future work is needed to determine the degree to which drought-tolerant species are confined to particular habitats. One would expect that in a more drought-prone climate, such drought-tolerant species may gain in abundance at the expense of others (Phillips *et al.* 2009, 2010; Feeley *et al.* 2011; Fauset *et al.* 2012). Further, studies to resolve the phylogenetic signal in π_{tlp} are needed to assess the evolutionary underpinnings of drought tolerance in tropical trees.

On the measurement of π_{tlp} and comparison across biomes

Our study is based on a novel approach for measuring leaf water potential at turgor loss point. It is based on the strong correlation of π_{tlp} with the osmotic potential at full hydration (π_o), easily measured with an osmometer. Previous studies suggest that this relationship stems from fundamental principles of leaf physiology, and consequently is robust to leaf type and habitat (Bartlett *et al.* 2012a, Bartlett *et al.* 2012b). Future studies can further test the robustness of this correlation and potentially refine the calibration equation by including points for more

species and vegetation types. In Appendix S1, we report raw osmometer π_o values in addition to π_{tlp} values to facilitate future calibration analyses.

The π_{tlp} values in our dataset were on average more negative than those previously reported in the literature for moist tropical forests (Fig. 1). There are several possible explanations for such a pattern, one of them being that previous studies tended to be conducted during the wet season, whereas we measured π_{tlp} at the peak of the dry season. Plants often acclimate π_{tlp} during drought periods, through the accumulation of cell solutes, or osmotic adjustment. Such an adjustment results in a lowering of π_{tlp} and can contribute to drought tolerance in vegetation worldwide (Wright *et al.* 1992; Abrams & Kubiske 1994; Cao 2000; Merchant *et al.* 2007; Zhu & Cao 2009; Bartlett *et al.* 2012b, 2014). The only previous study that reported a significant osmotic adjustment in a comparable moist tropical forest found an average adjustment of ca. 0.4 MPa for five species of *Psychotria*, a genus of understory plants (Wright *et al.* 1992), similar to the 0.5 MPa difference we found. However, in other reports, some moist tropical tree species did not present any osmotic adjustment (Wright *et al.* 1992; Cao 2000; Brodribb *et al.* 2003). Thus the lower mean π_{tlp} in this study may also reflect greater drought tolerance for species of the French Guiana tree flora compared with other moist tropical forests. Indeed, North-East Amazonia dried out repeatedly during the Holocene in a region that is today known as the Roraima corridor (extending from Para, Brazil, towards the Rupununi savannahs in Guyana, and including the Sipaliwini savannah; Mayle & Power 2008). Over long time scales, such repeated droughts may have induced shifts in the floristic composition of these forests, driven by strong ecological sorting of pre-adapted species through environmental filtering (Dick *et al.* 2013). Thus at least some elements of the flora of French Guiana may be able to better accommodate drought conditions than is currently assumed in most simulation models (Freycon *et al.* 2010).

On the status of π_{tlp} in the plant economics spectrum

In the literature, high sapwood density has often been considered as associated with drought tolerance, because trees with a lower vulnerability of the water transport system to stem embolism have been found to have denser wood (Hacke *et al.* 2001; Santiago *et al.* 2004; Markesteijn *et al.* 2011a; b). However, variation in sapwood density across various habitats and lineages of Amazonian rainforests appears to be less related to hydraulic function estimated from wood vessel anatomy and more closely associated with biomechanical support

as estimated by wood fibre composition (Fortunel *et al.* 2014; see also Chave *et al.* 2009; Zanne *et al.* 2010; Zieminska *et al.* 2013). The lack of a significant correlation between π_{tlp} and sapwood density in our dataset is further evidence that wood density is uncoupled from drought tolerance across phylogenetically and functionally diverse rainforest species.

The relationships between π_{tlp} and other leaf traits we found here, and in particular, the independence of π_{tlp} from leaf dry mass per area (LMA), reveal a disconnect of π_{tlp} from the leaf economics spectrum (Wright *et al.* 2004). The positive correlations between π_{tlp} and leaf toughness or thickness are at first sight counter-intuitive: they would suggest that a tougher or thicker leaf tends to be less drought tolerant. These results shed light on a long-standing controversy about the use of leaf structural traits as drought tolerance proxies. Higher values of LMA, leaf toughness and thickness as species traits have sometimes been found to be associated with drier conditions and thus proposed as potential predictors of leaf drought tolerance (e.g., Niinemets 2001; Lamont *et al.* 2002; Read & Sanson 2003; Wright *et al.* 2005; Poorter *et al.* 2009; Onoda *et al.* 2011). Although leaf toughness and thickness are associated with sclerophylly and often positively correlated with the leaf modulus of elasticity (ε), which reduces leaf shrinkage and dehydration under drought (Scoffoni *et al.* 2013), it has been recently demonstrated that neither of them play a direct role in drought tolerance globally, in particular because many drought sensitive species can have high LMA (Bartlett *et al.* 2012b). Here we confirmed that even within a given community, drought sensitive species may present either high or low LMA, and tougher and/or thicker leaves, probably in response to other evolutionary and environmental drivers, such as shade, nutrient availability or herbivory (see also Coste *et al.* 2005; Blackman *et al.* 2010; Markesteijn *et al.* 2011a). More generally, and as discussed elsewhere (Sack *et al.* 2003, 2013; Baraloto *et al.* 2010b; Reich 2014), LMA-related traits, including the leaf economics spectrum, tend to be independent of leaf- and plant hydraulic traits. In summary, soft traits commonly included in functional traits screenings and models, such as wood density and LMA, do not appear relevant to capture mechanistic drivers of tree growth response to environmental water stress and its species variability (Wagner *et al.* 2014).

We emphasize that π_{tlp} is a reasonably good proxy for a single, but key dimension of drought tolerance, i.e., maintaining gas exchange at strong transpiration rates and/or at negative soil water potentials, with a contribution to the prevention of cell shrinkage and consequent mechanical and metabolic damage. However, plants display a wide range of adaptations to delay or cope with these hazards. In particular, some species possess

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adaptations to delay or avoid the experience of drought in their tissues, in addition to, or instead of adaptations to maintain function during progressive drought: they mobilize stored water, develop a deep root system, limit gas exchange, or at the extreme shed leaves to stop leaf-level water exchange. Classically measured traits, such as deciduousness, already account, at least in part, for these alternative routes to drought tolerance. Future models integrating traits that reveal alternative means to drought tolerance will provide a more complete picture of plant resistance to drought and its variability.

Conclusion

Our study demonstrated strong variability in leaf drought tolerance across species, sites and environmental conditions. This variation illustrates how Amazonian plants' vulnerability to drought is poorly modelled in the plant functional types (Sitch *et al.* 2008) used by current dynamic global vegetation models (DGVMs). Such species variation is likely to be a source of discrepancy in models' simulations (Allen *et al.* 2010; Delbart *et al.* 2010; Joetzjer *et al.* 2013; Chave 2014). In particular, plant mortality is exclusively modelled through carbon balance in current DGVMs. However, plant survival should also depend on drought response and the stability of the hydraulic function (Tyree & Sperry 1989; Urli *et al.* 2013), the mobilization of non-structural carbohydrates and defence metabolism (McDowell 2011; Sevanto *et al.* 2014), all of which are poorly described (Powell *et al.* 2013; Xu *et al.* 2013). The new method we used is likely to be useful in conducting community-scale assessments of leaf-scale drought tolerance in the tropical tree flora. Our study suggests that, as already observed experimentally for relatively few species, important differences in drought tolerance are to be expected across evergreen species even in the Amazonian moist tropical forest vegetation zone, likely resulting in floristic composition changes. Our measure of drought tolerance, the leaf potential at turgor loss point (π_{tlp}), was found to be correlated weakly at best with typically used plant functional traits, and thus cannot be deduced easily from large existing plant functional trait repositories (Kattge *et al.* 2011). The integration of new trait-based information into models should shed crucial light on the still uncertain fate of the Amazon in response to climatic change. We propose that a more systematic measurement of π_{tlp}, integrated into the plant ecologist's toolkit of core plant functional traits that are routinely measured (Cornelissen *et al.* 2003), will significantly contribute to advancing this research agenda.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Dataset of estimated π_{osm} and π_{tlp} values for 165 trees in forests French Guiana

Figure S1. Correlation between leaf drought tolerance (π_{tlp}, in MPa) and several structural soft traits

Causes of variation in leaf-level drought tolerance within an Amazonian forest

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Chapter outline

This **Chapter 3** builds on the first exploration of the diversity of a drought tolerance trait, the leaf water potential at turgor loss point (π_{tlp}), presented in **Chapter 2** within an Amazonian forest community. An independent validation of the rapid method of π_{tlp} determination is conducted and a deeper exploration of π_{tlp} intra-specific and seasonal variability on a subset of species at our site is reported.

Abstract

Amazonian tree communities have already been seriously impacted by extreme natural droughts, and intense droughts are predicted to increase in frequency. However, our current knowledge of Amazonian tree species' responses to water stress remains limited, as plant trait databases include few drought tolerance traits, impeding the application and predictive power of models.

Here we explored how leaf water potential at turgor loss point (π_{tlp}), a determinant of leaf drought tolerance, varies with species life history, season, tree size and irradiance within a forest in French Guiana. First, we provided a further direct validation of a rapid method of π_{tlp} determination based on osmometer measurements of leaf osmotic potential at full hydration for five Amazonian tree species. Next, we analysed a dataset of 131 π_{tlp} values for a range of species, seasons, size (including saplings), and leaf exposure.

We found that early-successional species had less drought-tolerant leaves than late-successional species. Species identity was the major driver of π_{tlp} variation, whereas season, canopy tree size and leaf exposure explained little variation. Shifts in π_{tlp} from saplings to canopy trees varied across species, and sapling leaf drought tolerance was a moderate predictor of canopy tree leaf drought tolerance.

Given its low within-species variability, we propose that π_{tlp} is a robust trait, and is useful as one index of species' drought tolerance. We also suggest that measuring this trait would considerably advance our knowledge on leaf drought tolerance in hyperdiverse communities and would thus likely shed light on the resilience of such vulnerable species-rich ecosystem.

Keywords: osmotic adjustment, turgor loss point, wilting point, plasticity, ontogenetic shift, sun leaves, season

Introduction

Extreme natural droughts have already impacted on Amazonian ecosystem processes and services, through a decrease in tree growth and an increase in tree mortality (Phillips et al. 2009; Lewis et al. 2011; Marengo et al. 2011; Saatchi et al. 2013). In the future, such intense droughts are predicted to increase in frequency over Amazonia (Joetzjer et al. 2013; Boisier et al. 2015). Understanding and predicting the dynamics and responses to drought of Amazonian tree communities thus constitutes a crucial research challenge. We do know that plant water availability is a strong driver of tropical tree species distributions (Engelbrecht et al. 2007; Baltzer et al. 2008; Kursar et al. 2009; Comita & Engelbrecht 2009; Bartlett, Scoffoni, & Sack 2012; Fauset et al. 2012; Condit et al. 2013; Bartlett et al. 2015). However, our current knowledge of individual species' responses to water stress remains limited.

Plant functional traits are being increasingly used to explore the processes of plant community assembly (Kraft et al. 2008; Paine et al. 2011; Adler et al. 2013). Traits, such as leaf mass per area, wood density or seed size, are often used as predictors of tree growth trajectories and competitive intensity (Hérault et al. 2011; Lasky et al. 2015 ; but see Paine et al. 2015). Also plant traits play an increasing role in the development of dynamic vegetation models (Scheiter et al. 2013; Fyllas et al. 2014; Sakschewski et al. 2015). Global plant trait databases based on standardized protocols have been instrumental in such approaches (Cornelissen et al. 2003; Chave et al. 2009; Kattge et al. 2011; Pérez-Harguindeguy et al. 2013). However these databases include limited information about the hydraulic functioning of plants, reflecting a historical bias of functional ecology towards the understanding of photosynthesis, wood mechanics, or plant architecture. A major recent effort to compile a stem hydraulic trait database has already highlighted the global vulnerability of forest trees to drought (Choat et al. 2012). Such trait data are essential, as there is growing evidence that often measured plant traits, such as leaf mass per area or wood density, correlate poorly with plant hydraulic responses or drought tolerance (Sack et al. 2003; Sack et al. 2013; Li et al. 2015; Gleason et al. 2015; Maréchaux et al. 2015), though they may be related within given communities, e.g., for drought-sensitive pioneers versus drought-tolerant late-successional species within given forests (Markesteijn, Poorter, Bongers, et al. 2011; Markesteijn, Poorter, Paz, et al. 2011). This situation impedes the application and predictive power of trait-based modelling (Wright et al. 2010; Wagner et al. 2014; Paine et al. 2015). Here, we contribute to filling this gap by exploring how the leaf water potential at wilting point, a classical leaf

drought tolerance trait, varies across species, seasons, sizes and leaf exposure, in a tropical forest.

The leaf water potential at turgor loss point (π_{tlp}, in MPa) is the negative water potential at which the leaf wilts. It also corresponds to the soil water potential below which the plant cannot take up sufficient water to recover overnight from wilting after a day of transpiration. Leaves with a more negative π_{tlp} maintain critical processes such as leaf hydraulic conductance under drier conditions, contributing to greater plant drought tolerance (Cheung et al. 1975; Abrams et al. 1990; Brodribb & Holbrook 2003; Bartlett, Scoffoni, & Sack 2012; Guyot et al. 2012). π_{tlp} is a good predictor of species distributions relative to water supply (Lenz et al. 2006; Bartlett, Scoffoni, & Sack 2012; Bartlett et al. 2015). Recently, we found that tropical forest tree assemblages display substantial species variation in π_{tlp}, with some species being surprisingly drought-tolerant (Nepstad et al. 2007; da Costa et al. 2010; Maréchaux et al. 2015). This study relied on a new protocol for π_{tlp} determination that is an order of magnitude faster than the classic pressure-volume curve method (Bartlett, Scoffoni, Ardy, et al. 2012), based on a well-established correlation of π_{tlp} with the leaf osmotic potential at full hydration, measurable with an osmometer (Sack et al. 2003; Lenz et al. 2006; Blackman et al. 2010; Scoffoni et al. 2011; Bartlett, Scoffoni, & Sack 2012). Here, we provide the first direct validation of this rapid method of π_{tlp} determination for Amazonian tree species.

The potential associations of the leaf water potential at wilting point with other ecological factors than species have seldom been explored (Choat et al. 2007). Working within a diverse Amazonian forest in French Guiana, we sought to resolve the role of the following ecological factors, which have been hypothesized but not previously tested to drive the variation in leaf drought tolerance, at multiple scales, including across species, within species across individuals, and within individual crowns. Across species, early-successional species have been predicted to show trait values that maximize resource gain at the expense of stress tolerance (Markesteijn, Poorter, Bongers, et al. 2011; Markesteijn, Poorter, Paz, et al. 2011; Reich 2014), leading us to expect these species would have less negative π_{tlp} values than late-successional species (hypothesis i). Seasonal variation in water supply is a major driver of intraspecific variation in π_{tlp} for species from diverse ecosystems worldwide, with osmotic adjustment, or the accumulation of cell solutes, acting across time scales from days to seasons to acclimate π_{tlp} to more negative values during water stress (Bartlett et al. 2014). This drought-tolerance mechanism has never been explored for Amazonian tree species, but we expected to see significant seasonal changes in π_{tlp} for our study species (ii). In closed-

canopy tropical forests, intraspecific trait variation is often driven by the strong light gradient within the canopy (Niinemets 2010). Emergent trees withstand greater heat and excess light stress and higher evaporative demand leading us to predict that drought tolerance would vary across tree sizes, with larger canopy trees showing more negative π_{tlp} values than smaller canopy trees (iii), and canopy trees showing more negative π_{tlp} values than saplings of the same species (iv). Consistent with hypothesis iii, some studies reported tall trees to be more vulnerable to drought than smaller trees (Van Nieuwstadt & Sheil 2005; Nepstad et al. 2007; da Costa et al. 2010; Phillips et al. 2010; Rowland et al. 2015), although others did not (Enquist & Enquist 2011; Feeley et al. 2011; Fauset et al. 2012). Disentangling the potential structural and physiological causes of these opposed trends has proven difficult (Niinemets 2010). To our knowledge, variation in π_{tlp} has never been compared between mature trees and saplings. Canopy trees often include both shade and sun leaves, the latter being more exposed to heat light and evaporative stress and differing predictably in a number of structural and physiological traits (Sack et al. 2003; Rozendaal et al. 2006; Sack et al. 2006; Markesteijn et al. 2007). We thus predicted sun leaves would show greater drought tolerance, and thus more negative π_{tlp} values than shade leaves within the crown of a single tree (v).

Material and methods

Study sites and sampling strategy

Field measurements were conducted at the Nouragues Ecological Research Station in French Guiana. It is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05' N, 52°40' W; Bongers *et al.* 2001). The site receives c.a. 3000 mm/yr rainfall, with significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. A long wet season lasts from December to July, often interrupted by a short dry period in March. The dry season lasts from the end of August to November with 2-3 months with precipitation <100 mm/mo (Bongers et al. 2001). Data were collected in a 12-ha permanent forest plot on clay-sand soil (Petit Plateau). The permanent plot was fully censused in 2012, all trees ≥10 cm diameter at breast height (DBH) were identified and their DBH measured. Within the 12-ha plot, richness is in excess of 600 tree species (C Baraloto, J Engel, P Pétronelli, unpublished results).

Measurements of leaf water potential at turgor loss point (π_{tlp}) were conducted in September 2012 and September 2015 during two dry seasons, and in May 2014 in the middle of the wet season (Appendix S1). The cumulative rainfall 30 days prior the ending date of each sampling session, based on logging half-hourly data at the site (Campbell Scientific SBS500, Shepshed, Leicestershire, UK), was 21 mm, 78 mm and 265 mm for the 2012 dry season, the 2015 dry season, and the 2014 wet season respectively. Ten focal species were selected that were relatively abundant in the study plot to maximize the range in π_{tlp} (Maréchaux et al. 2015). Three to eleven canopy trees were sampled per species in each season (Table 1). Small branches were collected by climbing the trees using French spikes (Fonderies Lacoste, Excideuil, France; de Castilho et al. 2006) or using the single-rope technique (Anderson et al. 2015). For 19 of the 56 canopy trees sampled during the wet season, both sun and shade leaves could be sampled. For five of the ten focal species, saplings (individuals with a height typically less than 1.50m, thus growing in the understory) could be easily identified, and three to seven saplings were sampled per species during the wet season in May 2014 (n=24 saplings total; Table 1).

Estimating π_{tlp} using the osmometer method

We assessed the leaf turgor loss point, π_{tlp}, from a previously established linear relationship with the osmotic potential at full hydration (π_o), in turn directly measured with a vapour pressure osmometer (Vapro 5520, Wescor, Logan, UT; Bartlett *et al.* 2012a). Henceforth, we refer to this technique as the osmometer method.

Branches were collected from the selected trees and placed in opaque bags with wet paper towel, then recut under water at least two nodes distal to the original cut and allowed to rehydrate overnight covered with plastic, and branch ends underwater. Three mature leaves were collected from each rehydrated branch and stored in Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA) with a wet paper towel. One disc was sampled from each leaf centrally between the midrib and margin with an 8-mm-diameter cork borer, excluding first- and second-order veins to avoid too much apoplastic dilution that would lead to less negative osmometer values (Kikuta & Richter 1992). However, for one focal species, *Qualea rosea* (Vochysiaceae), a dense secondary venation disallowed excluding them. The discs were wrapped in foil and frozen by immersion in liquid nitrogen (LN_2) for at least 2 minutes, then immediately punctured 10-15 times with sharp-tipped forceps and sealed in the osmometer chamber, using the standard 10 μL chamber well. The discs were exposed to air for less than

40 seconds for all steps between removing the leaf from the Whirl-Pak bag and sealing the disc in the osmometer. The equilibrium solute concentration value c_0 (in mmol kg^{-1}) was recorded from the osmometer when the difference between consecutive 2-minute measurements fell below 5 mmol kg^{-1}. This value was converted to π_o values from the osmometer (π_{osm}) using the van't Hoff equation relating solute concentration to vapour pressure:

$$\pi_{osm} = -\frac{2.5}{1000} \times c_0 \tag{1}$$

where the numerator of the first term represents $R \times T$ = 2.5 L MPa mol^{-1} at 25°C, with R the ideal gas constant and T the temperature in Kelvin degrees.

The value π_{osm} was then converted into π_{tlp} using the previously published regression equation relating π_{osm} to pressure-volume curve turgor loss point values (π_{tlp-PV}; Bartlett, Scoffoni, Ardy, et al. 2012). This regression was developed from woody species representing a wide range of leaf structural features and habitat preferences (n=30 species, R^2=86%, p<2.10^{-12}, π_{osm} range=[-3.03, -0.64] MPa and π_{tlp-PV} range=[-3.00, -1.02] MPa) and was:

$$\pi_{tlp} = 0.832 \times \pi_{osm} - 0.631 \tag{2}$$

This reference regression is based on fundamental equations describing biophysical processes and should therefore hold universally across species. However, we sought to further validate this equation for Amazonian tree species.

Validating the osmometer method for Amazonian tree species

To this end, we calculated the water potential at turgor loss point using the pressure-volume curve method (henceforth denoted the PV curve method; π_{tlp-PV}) and also measured π_{osm} with the osmometer method on the same individuals from six species (n=18 individuals and 6 species). Our validation was conducted in September 2015. Species were excluded if they produce foliar latex or resin, known to create problems with the PV curve method. Branches were allowed to rehydrate overnight as above. Five to six leaves from three individuals per species were dried on a laboratory bench and repeatedly weighed (using a Ohaus Scout Pro Balance SPU 123, Parsippany, NJ, USA) and measured for water potential with a pressure chamber with a digital gauge (PMS Instrument Co., Corvallis, OR, USA). Leaf dry mass was determined after 72 h at 70°C in a drying oven. π_{tlp-PV} was calculated from the relationships between water potential and water content (Koide et al. 2000; Sack et al. 2011). Species-level π_{tlp-PV} was computed as the average of π_{tlp-PV} values of the 5-6 leaves from that species. All π_{osm} and π_{tlp-PV} values are available (Appendix S2).

We compared the root mean squared error (RMSE) from Equation (2) computed for the published calibration dataset (n=30 species; Bartlett et al., 2012) and for the dataset including the six additional species in this study (n=6 and n=36 species). RMSE was computed as follows:

$$RMSE = \sqrt{\frac{1}{n}\sum_n (\pi_{tlp} - \pi_{tlp-PV})^2} \qquad (3)$$

where π_{tlp} values were turgor loss point estimates with Equation (2). We identified potential outliers in the merged dataset (n=36 species) using jackknife resampling method with RMSE as statistics (R package *bootstrap*; Tibshirani & Leisch 2015). We also fitted the 6-species and the merged dataset and compared the 95% confidence intervals of slope and intercept of the 6- and 36-species datasets with the 30-species dataset based on 1000 bootstraps (R package *boot*; Canty & Ripley 2013).

Data analyses

All analyses were conducted for the wet-season π_{tlp} values (May 2014), except for the comparison between seasons. We considered the mean of the sun and shade leaves π_{tlp} values for individuals for which both were collected, excepted when comparing leaves sampled at different light exposures. Also, for reasons explained below, individuals from one species, *Qualea rosea*, were excluded from all subsequent tests.

To test for species differences in π_{tlp} values, we used linear models (ANOVA), with species as a fixed effect, and Tukey HSD tests for pairwise species comparisons. The relative contribution of within- and across-species differences to π_{tlp} variability was quantified by partitioning variance (Sokal & Rohlf 1987). We also tested for differences in π_{tlp} between species grouped into early-successional, mid-successional and late-successional species according to field observations (Table 1), using an ANOVA, with successional status as a fixed effect, and Tukey HSD for post hoc pairwise comparisons.

We compared wet-season canopy tree values with dry-season values with the same osmometer method (Maréchaux et al. 2015) for six species with at least three individuals sampled during each season. We tested for a seasonal effect using a two-way ANOVA with season and species as fixed effects and using t-tests for each species.

Using DBH as a proxy for tree size, we investigated the relationships between canopy tree DBH and π_{tlp}, and repeated this analysis accounting for the species effect (linear regressions between DBH and residuals of the ANOVA on π_{tlp} with species as a fixed effect) to exclude variability caused by species differences in stature. We also tested differences in

π_{tlp} for four species for which we sampled both canopy trees and saplings, using a two-way ANOVA (type II) with size (categorical: sapling/canopy) and species as fixed effects.

We tested differences in π_{tlp} between leaves collected in full sunlight at top canopy height (henceforth denoted sun leaves) and leaves collected in shaded conditions lower in the canopy (shade leaves) within individuals using a paired t-test (n=18 individuals). We validated our classification of sun and shade leaves by testing for differences in additional traits known to vary with light environments (Niinemets et al. 2015), i.e., leaf mass per area ($P<10^{-4}$, mean of the differences=15.3 g.m^{-2}), and carbon isotope ratio ($P<10^{-3}$, mean of differences=1.23 ‰; data not shown).

All statistical analyses were conducted using the R software (R Core Team 2013) and preceded by normality and homoscedasticity tests when required, using Shapiro-Wilk test, Bartlett test or Levene test (*car* package; Fox & Weisberg 2011).

Results

Model validation with Amazonian tree species

The species *Qualea rosea*, with its dense secondary vein network was clearly identified as an outlier: for this species, the PV-curve value of π_{tlp} value was much lower than that obtained with the osmometer method (π_{tlp}- $\pi_{\text{tlp-PV}}$=0.58 MPa). We decided to remove this outlier species from all subsequent analyses. The RMSEs of the 5- and 35-species datasets were both 0.18 MPa, equal to that of the previously constructed 30-species model (Bartlett et al., 2012). 95% confidence intervals of the slope and the intercept of both of the 5- and 35-species regressions included the parameter estimates for the previous 30-species calibration. The new correlation between π_{osm} and $\pi_{\text{tlp-PV}}$, established based on the 35 species was

$$\pi_{tlp} = 0.799 \times \pi_{\text{osm}} - 0.665 \qquad (4)$$

($P<10^{-14}$, R^2=0.85, RMSE=0.18 MPa, Fig. 1). We conclude that this relationship is applicable to Neotropical trees, as assumed previously (Maréchaux et al. 2015), provided the leaf secondary vein network is not too dense.

Cross-species variation in π_{tlp}

The π_{tlp} of canopy trees varied across species (Table 1, Fig. 2; ANOVA, P<1.10^{-15}), with 87% of the variance in π_{tlp} associated with species differences (n=9 species and 50 individuals). Early-successional (n=2 species and 11 individuals) exhibited significantly less negative π_{tlp} values than mid-successional species (n=2 species and 10 individuals). In turn, mid-successional species exhibited less negative π_{tlp} values than late-successional species (n=5 species and 29 individuals; ANOVA P<1.10^{-7}, Tukey HSD tests: all P<0.05; Fig. 3).

Seasonal and size-related variation in π_{tlp} within species

We found no difference between dry- and wet-season π_{tlp} for any of the tested tree species (n=6 species; two-way ANOVA; t-tests: all p-values > 0.3, Table 1, Fig. 2). This was still the case when excluding data collected during the September 2015 sampling session which was less dry than the particularly stressed period of September 2012.

The π_{tlp} was not statistically related to DBH among canopy trees (linear regression, P=0.44, n=50 individuals). Further, DBH did not explain residual π_{tlp} variance among canopy trees after accounting for the species effect (linear regression between DBH and the residuals of ANOVA on π_{tlp} with species as a fixed effect, P=0.43). This result also held when excluding individuals growing in large open gaps (n=7 species and 37 individuals, P=0.48), for which a variation in size may not result in a variation in abiotic stresses due to changes of vapour pressure deficit, temperature or light intensities.

Species, plant stature (canopy vs sapling) and the interaction of these two effects had a significant effect on π_{tlp} (two-way ANOVA, n=4 species, all P≤0.05, range of average π_{tlp} differences between stature within species: [-0.23, -0.11] MPa). For all species, canopy trees displayed a more negative π_{tlp} than saplings, except the early-successional *Pourouma sp.* which showed the opposite pattern (Table 1, Fig. 2).
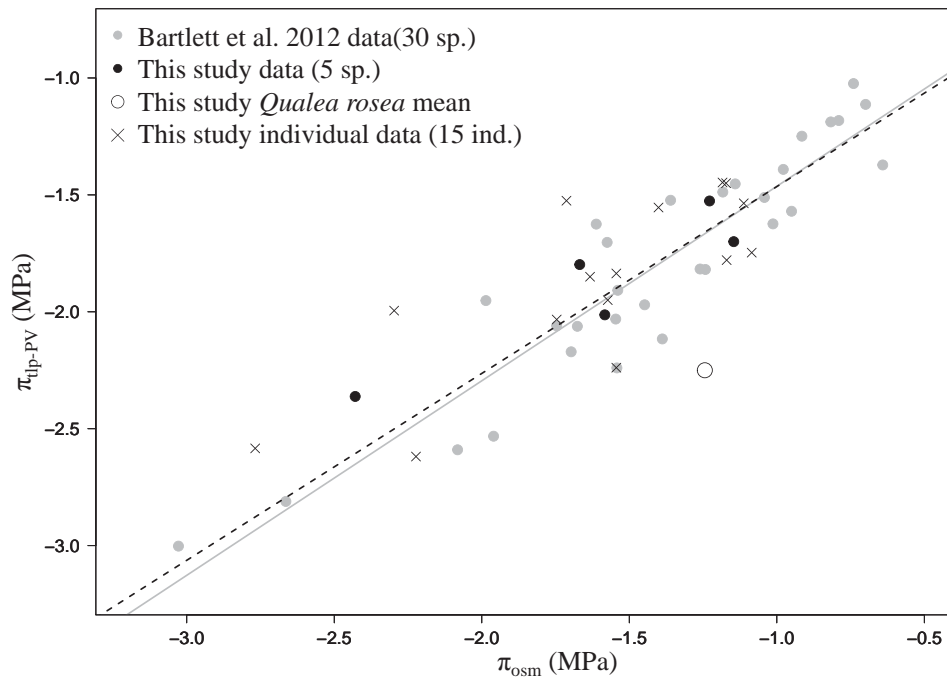
Fig. 1. Validation of the osmometer method for Amazonian tree species. Linear regressions between species leaf water potentials at turgor loss point measured with the PV curve method ($\pi_{tlp\text{-}PV}$, in MPa) and species osmotic potentials at full hydration measured with an osmometer (π_{osm}, in MPa), for the (Bartlett, Scoffoni, Ardy, et al. 2012) 30 species means (solid line) only and including the five species in this study (excluding *Qualea rosea*, 35 species, dashed line). The regressions were not significantly different.

Table 1. Mean and standard error of π_{tlp} values in wet and dry seasons and for saplings and canopy trees.

| Species | Type | | WET SEASON | | | | DRY SEASON | |
| | | | Canopy trees | | Saplings | | Canopy trees | |
		n	π_{tlp}	n	π_{tlp}	n	π_{tlp}	
Protium gallicum	LS	6	-2.52 ± 0.05	3	-2.29 ± 0.20	4	2.50 ± 0.10	
Voucapoua americana	LS	6	-2.17 ± 0.06[c]			6	-2.15 ± 0.08	
Goupia glabra	MS	4	-2.09 ± 0.03[c]			3	-2.02 ± 0.05	
Licania alba	LS	7	-2.03 ± 0.05[c]	6	-1.83 ± 0.04	11	-2.01 ± 0.04	
Cyrillopsis paraensis	LS	5	-2.00 ± 0.03[cf]					
Eschweilera coriacea	LS	5	-1.76 ± 0.08[bef]			11	-1.76 ± 0.05	
Pourouma sp.	ES	3	-1.54 ± 0.10[abd]	3	-1.76 ± 0.10			
Dicorynia guianensis	MS	6	-1.52 ± 0.04[abd]	6	-1.41 ± 0.03	10	-1.66 ± 0.08	
Cecropia obtusa	ES	8	-1.43 ± 0.04[a]					

ES: early-successional; MS: mid-successional; LS: late-successional.
Same lower case letters indicate a non-significant difference between species values for canopy trees (Tukey test: P>0.05).
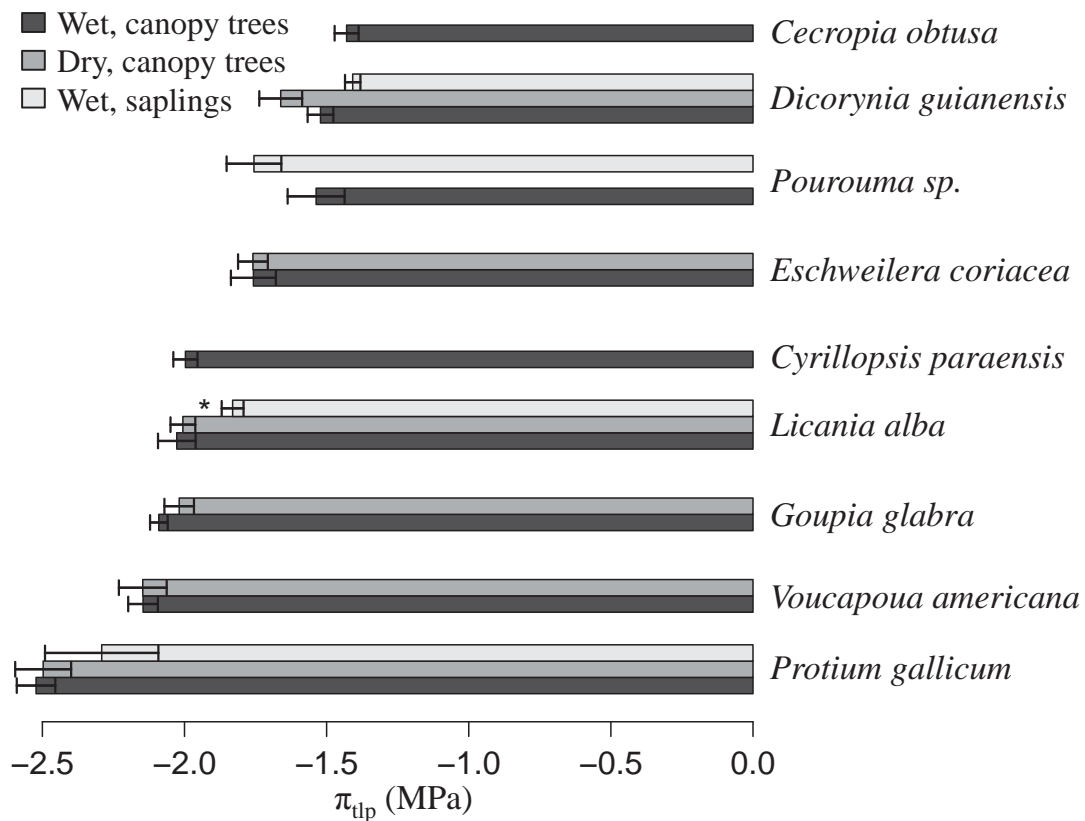
Fig. 2. Leaf water potential at wilting point (π_{tlp}, in MPa) across species in our dataset, with mean ± standard error for species wet-season canopy tree (black), dry-season canopy tree (dark grey) and wet-season sapling (light grey) values. * indicates significant differences between saplings and canopy trees during the wet season within species (t.test : P<0.05).

Fig. 3. Differences in leaf water potential at wilting point (π_{tlp}, in MPa) across successional stages, for early-, mid- and late-successional canopy trees (n=11, 10 and 29 individuals respectively). Means ± standard errors are reported. Different lower case letters indicate a significant difference between stages (Tukey test: P<0.05).

Intra-crown variation in π_{tlp}

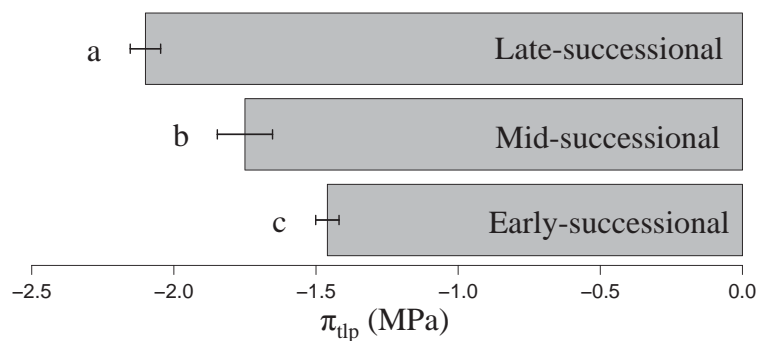Differences between sun and shade leaves within individuals were marginally significant, remaining lower than the model's RMSE (paired t-test, P=0.05, mean of the differences=-0.09 MPa, 95% confident interval of the difference= [-0.18 ; -0.00] MPa; n=18 individuals; Fig. 4).
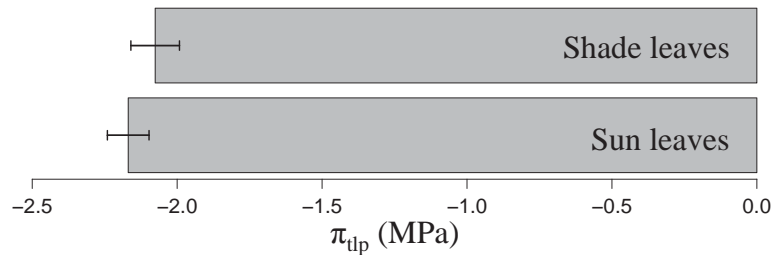
Fig. 4. Comparison between sun and shade leaves leaf water potential at wilting point (π_{tlp}, in MPa) for 18 tropical canopy trees, with mean ± standard error.

Discussion

Validation of the osmometer method for Amazonian tree species

We applied a rapid method of leaf turgor loss point determination based on osmometer measurements of leaf osmotic potential at full hydration (π_{osm}). The correlation between π_{osm} and π_{tlp} was initially established for 15 species sampled in gardens adjacent to the campus of University of California, Los Angeles, from vegetation zones ranging from chaparral to tropical wet forest, and a further 15 species growing in natural conditions in a Chinese tropical rainforest (Bartlett, Scoffoni, Ardy, et al. 2012). These two subgroups did not differ statistically in the relationship between measurement methods, consistent with the expectation that because the relationship is biophysically based, it can be applied across vegetation zones (Bartlett, Scoffoni, Ardy, et al. 2012). Here, we included five more species from canopy tropical trees, and confirmed the strong consistency of the correlation, lending further credence to the proposal that it can be applied universally across angiosperm species. Model error remained consistently low after adding the new species. Indeed, the new correlation was not significantly different from the previously established one. We thus conclude that the original model, or its slight improvement reported in Equation (4), can be reliably used to infer leaf-level potential at wilting point across a wide range of angiosperm species.

The rapid method offers invaluable opportunities to better inform and quantify the diversity of leaf drought tolerance in such vulnerable species-rich plant communities. The π_{tlp} has been used as a proxy for general plant drought tolerance, because in several species sets it was notably correlated with specialization of species between wet and dry forests and biomes (Bartlett, Scoffoni, & Sack 2012) and the water potential at stomatal closure (Brodribb et al. 2003; Brodribb & Holbrook 2003; Blackman et al. 2010), even though more research is required to further elucidate the mechanistic relationships among traits which could potentially arise due to mechanistic linkage and/or to simultaneous co-selection during evolution, e.g., for performance under a given moisture availability regime. Besides, in particular for tropical tree species, the measurement of xylem resistance to cavitation is challenging because of the presence of long vessels (Martin-StPaul et al. 2014; Torres-Ruiz et al. 2014 ; Delzon 2015), and few measurements of the xylem pressure at which 50% loss of conductivity occurs (P_{50}) are available, although these trait was correlated with π_{tlp} in several data sets (Choat et al. 2007; Blackman et al. 2010; Fu et al. 2012). Nine published P_{50} values for tree genera present at our site were reported in the global database of Choat et al. (2012), including six genera collected at the Parque Nacional San Lorenzo, Panama and three genera at La Selva Research Station, Costa Rica. The range of P_{50} values ([-2.70; -1.00] MPa) was comparable to the range of π_{tlp} values found at our site (this study: [-2.52; -1.43] MPa and Maréchaux et al. 2015: [-3.15; -1.41] MPa). Since π_{tlp} is currently the only easily measurable drought tolerance trait for tropical woody angiosperms, it is important to further explore the relationship between P_{50} and π_{tlp} for these species.

One species, *Qualea rosea*, departed from the model's predictions. This species displayed a dense network of leaf secondary veins, and the osmometer method led to an over-estimated (less-negative) turgor loss point value. This is consistent with previous studies finding that including secondary veins in a sample leads to a greater apoplastic dilution and thus less negative osmometer measurements (Kikuta & Richter 1992). Species with very dense secondary vein networks should be carefully excluded when using this method. In the French Guiana flora, the number of species with dense secondary venation is limited: only about 2.5% of the tree genera, and <2% of tree species contain species with a dense secondary venation (J Engel, personal communication).

Variation in π_{tlp} strongly determined by species identity and life history

Species identity was the major determinant of leaf drought tolerance, and inter-specific variation in π_{tlp} was larger than intra-specific or intra-individual variation. In contrast, season, canopy tree size or leaf light exposure did not explain much of this variability.

Species identity explained 87% of the variance of π_{tlp} in our dataset (n=9 species, 50 individuals), a larger proportion than previously found (40 %, n=13 species, 82 individuals; Maréchaux et al., 2015). This result is in agreement with previous studies in other ecosystem types (Lenz et al., 2006; Bartlett et al., 2015). Overestimation of interspecific variation in plant traits may result from standardized protocols minimizing intraspecific variation (Cornelissen et al. 2003; Violle et al. 2012). However, this alone could not explain our pattern since our leaf sampling was not standardized with respect to light exposure or canopy tree size and was designed to maximise the entire range of the selected species. We acknowledge that we sampled species at a single site which may induce a lower intra-specific variability than if we had sampled across many sites (Hulshof & Swenson 2010; Albert et al. 2010; Siefert et al. 2015). However in a previous study, variation as assessed at two sites did not result in a greater intraspecific variation in π_{tlp} (Maréchaux et al. 2015).

As hypothesized from a whole-plant "fast-slow" economics spectrum (Reich 2014) and reported coordination of species' drought and shade tolerance (Markesteijn, Poorter, Bongers, et al. 2011; Markesteijn, Poorter, Paz, et al. 2011), early-successional species tended to exhibit less negative π_{tlp} values than later-stage species. This is in agreement with light-demanding species showing higher maximum stomatal conductance and assimilation and transpiration rates than shade-tolerant species under well-watered conditions, but a stronger sensitivity of these variables to soil drought, probably due to a more sensitive stomatal control on average in early-successional species (Huc et al. 1994; Bonal et al. 2000).

Absence of seasonal osmotic adjustment

We found no seasonal adjustment in π_{tlp} for the five species with both dry and wet seasons values in our dataset. This result reinforces the view that some tree species in French Guiana are far more drought-tolerant than previously assumed for moist tropical forests, perhaps due to adaptation to past and recurring drought events in the region (Maréchaux et al. 2015). This finding runs contrary to what was expected from a global meta-analysis that reported consistent and prevalent seasonal plasticity in π_{tlp} across 246 species from eight biomes

worldwide (Bartlett et al. 2014). However, that meta-analysis also concluded that there is a wide variability in plasticity across species. The few existing studies that reported tropical moist species π_{tlp} values across seasons provided mixed evidence for osmotic adjustment in tropical tree leaves (Wright et al. 1992; Cao 2000; Brodribb et al. 2003).

One reason explaining the absence of osmotic adjustment in our dataset could be that dry seasons rarely result in a strong tree physiological stress in French Guiana. Values of predawn and midday leaf water potentials measured during an average dry season (Stahl et al. 2011; Stahl et al. 2013) usually were less negative than π_{tlp} values reported at the same site (Maréchaux et al. 2015): at the end of the dry season in November 2007, the range of predawn leaf water potentials were [-1.30;-0.15] MPa, 75% of which were less negative than -0.45 MPa (n=64 individuals), while the range for midday leaf water potentials were [-2.95;-0.60] MPa, 75% of which were less negative than -1.90 MPa (n=49 individuals; C Stahl personal communication). Thus, we do not exclude the possibility of osmotic adjustment under harsher droughts.

π_{tlp} does not depend on canopy tree size, but differs for saplings

In agreement with our prediction, we found that canopy tree size did not have a significant effect on π_{tlp}, whether through a species effect or within species. This finding is interesting in light of studies that have suggested a higher vulnerability to drought of large trees compared with smaller trees (Van Nieuwstadt & Sheil 2005; Nepstad et al. 2007; da Costa et al. 2010; Phillips et al. 2010; Bennett et al. 2015), although this pattern was not observed in other studies (Enquist & Enquist 2011; Feeley et al. 2011; Fauset et al. 2012). Emergent trees are indeed exposed to greater atmospheric evaporative demand and hydraulic constraints. However, these large trees can also store larger amounts of water and thus withstand prolonged periods of stomatal closure (Goldstein et al. 1998; Meinzer et al. 2008), compete strongly for soil resources with their large root systems and access the water table deeper down (Nepstad et al. 1994; Dawson 1996; Ivanov et al. 2012; but see Meinzer et al. 1999; Markewitz et al. 2010; Stahl, Herault, et al. 2013), and accumulate more non-structural carbohydrates that may help maintain high osmotically active compound concentrations and thus attenuate the effect of drought (Sala & Hoch 2009; Woodruff & Meinzer 2011; Sala et al. 2012; O'Brien et al. 2014 ; but see Rowland et al. 2015).

Our results indicate that tall tropical trees do not have a higher leaf-level drought tolerance relative to smaller trees. This in turn suggests that large trees are not more

vulnerable to drought than smaller trees. However we found evidence for a weak shift in leaf drought tolerance between saplings and canopy trees. Notably, early- and late-successional species showed opposed trends in their variation in π_{tlp} between saplings and trees, although not all were significant in our dataset of limited sample size. In the late-successional species, leaves of saplings were less drought-tolerant than those of canopy trees. In contrast, for species growing in gaps, leaves were more drought-tolerant at the sapling stage. Such contrasting shifts from saplings to canopy trees across species suggest that these species operate under differential ecophysiological constraints. Differential ability to cope with drought across plant sizes has been reported in relation to changes in environmental constraints (Donovan & Ehleringer 1991; Donovan & Ehleringer 1992; Cavender-Bares & Bazzaz 2000; Niinemets 2010). Soil water availability also differs between gaps and the understory: gaps are more controlled by the evaporation of soil surface while closed-canopy forest soil water is depleted by dense root water extraction below the surface (Becker et al. 1988; Marthews et al. 2008). Saplings of early-successional species, growing in gaps, with typically more superficial roots than taller individuals despite similar high-light exposure, may thus be strongly stressed even during short dry spells in the wet season (Engelbrecht et al. 2006). On the contrary late-successional saplings, growing in closed understory, may be more strongly impacted by herbivory and thus invest more in leaf defense against herbivores than in drought tolerance (Coley & Barone 1996). It would be useful to increase sample size to further analyse these trends, as the contribution of shifts in π_{tlp} to defining the ecological niche of plant species seems to be a promising research avenue.

A weak variation in π_{tlp} across leaf exposure within tree canopy

Sun leaves showed structural and physiological acclimation to high radiation loads and high vapour pressure deficit, with typically higher mass per area and nutrient concentration per area than shade leaves, as expected from previous studies (Sack et al. 2003; Rozendaal et al. 2006; Sack et al. 2006; Markesteijn et al. 2007; Hulshof & Swenson 2010; Weerasinghe et al. 2014). However, we found no substantial differences in absolute π_{tlp} values between sun and shade leaves just as reported previously for temperate woody species (Sack et al. 2003). A strong acclimation in traits related to maximum flux of water and carbon through the leaf, such as leaf hydraulic conductance, vein density, and photosynthetic gas exchange may occur alongside little acclimation in traits associated with leaf drought tolerance (Sack et al. 2003; Sack & Holbrook 2006).

On measuring the community-wide leaf water potential at turgor loss point

The rapid technique of π_{tlp} determination validated here for Amazonian tree species opens new possibilities for studying drought tolerance within and across species. This gives access to a key drought tolerance trait as part of the plant ecologist's toolkit of routinely measured functional traits (Cornelissen et al. 2003). We propose that it should now be possible to survey the π_{tlp} in hyperdiverse communities and thus shed light on both the resilience of this ecosystem and on how the Amazonian flora has been assembled.

We found that species identity was the main driver of π_{tlp} values with early-successional species being less drought-tolerant than later-successional species, and that season, canopy tree size and leaf exposure contributed relatively negligible variation. Yet, we explored only some of the factors that might affect inter-individual variability, species plasticity, and species differences. For instance we did not study the effect of topography (Silva et al. 2013; Liu et al. 2014) or species maximum height (Poorter et al. 2005). Intra-specific variability, whatever the drivers, may have direct consequences on sampling design and effort for community-wide measurements. However, our result confirms that π_{tlp} could be used as a suitable species-level trait of tree drought tolerance, thus considerably simplifying sampling and determination of drought tolerance in species-rich communities (Baraloto et al. 2010).

We also provided evidence of an ontogenetic shift in π_{tlp} that is variable across species. Particular care should thus be taken when scaling to canopy trees leaf-level drought tolerance measurements based only on saplings (Engelbrecht et al. 2007; Kursar et al. 2009). More research is needed to elucidate how such a variation across ontogeny and across species may impact species performance and vital rates across the life cycle (Adler et al. 2014) and under multiple stresses (Niinemets 2010).

Acknowledgments

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Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an Amazonian forest

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Chapter outline

The exploration of the diversity of leaf-level drought tolerance within an Amazonian forest community presented in **Chapters 2 and 3** focused on trees. However lianas are abundant in tropical forests. Across the tropics lianas have been found to increase in abundance with decreasing rainfall and increasing seasonality. They may thus be particularly favoured under increasing drought intensity and frequency. A liana growth advantage over trees under dry conditions has been advanced to explain these patterns, but has so far received little robust physiological explanations. In this **Chapter 4,** a novel potential explanation is explored by comparing the leaf water potential at turgor loss point of lianas and trees across seasons.

Abstract

Pan-tropically, liana density increases with decreasing rainfall and increasing seasonality. This pattern has led to the hypothesis that lianas display a growth advantage over trees under dry conditions. However the physiological mechanisms underpinning this hypothesis remain elusive. A key trait influencing leaf and plant drought tolerance is the leaf water potential at turgor loss point (π_{tlp}). π_{tlp} adjusts under drier conditions and this contributes to improve leaf drought tolerance. For co-occurring Amazonian trees (n=247) and lianas (n=57) measured during the dry and the wet seasons, lianas showed a stronger osmotic adjustment than trees. Liana leaves were less drought-tolerant than trees in the wet season, but reached similar drought tolerances during the dry-season. Stronger osmotic adjustment in lianas would contribute to turgor maintenance, a critical prerequisite for carbon uptake and growth, and for the success of lianas relative to trees in growth under drier conditions.

Keywords: drought tolerance, wilting point, plasticity, functional traits, lianas, leaf water potential

Introduction

Over the past decades, lianas have been increasing in abundance in tropical forests [1]. Across the tropics, liana density and biomass tend to increase with decreasing rainfall and increasing seasonality [2]. These two patterns have led to the hypothesis that lianas display a dry season growth advantage over trees. In support of this hypothesis, Schnitzer [3] found that lianas grow significantly more than trees during the dry season relative to the wet season in a tropical forest of Panama. However the physiological mechanisms underpinning this lianas dry-season advantage remain elusive.

One explanation is that lianas have a deeper root system than co-occurring trees, enabling them to access soil water when the upper soil layer dries out. Indeed, lianas would seem capable of investing more into root development, since they need to allocate fewer resources than trees to stem support. However, the few empirical comparisons of root depth have thus far provided mixed or contradictory results [4,5]. Another possibility is that lianas may benefit from higher light intensity in the dry season, since their leaves are on average higher in nutrient concentrations and photosynthetic capacities than trees at some sites, though not at others [4]. Additionally, stronger stomatal control in lianas [5] may result in stronger reduction in carbon assimilation during dry periods. Other aspects of the water transport system do not show a clear advantage for lianas. Even though lianas consistently show wider vessels than trees and higher stem-specific hydraulic conductivities, their larger leaf area and longer stem may lead to lower leaf-specific conductivity [4]. Additionally, lianas tend to be more vulnerable than trees to drought-induced cavitation [4]. Overall, evidence for a physiological advantage of lianas under a seasonally dry environment has been elusive.

Here, we explore a new hypothesis. When plants are water-stressed, the first response is the reduction of turgor-driven cell expansion and division hence growth [6]. Leaf cell turgor also controls stomatal dynamics and thus plant water regulation [7]. A key leaf drought tolerance trait is the leaf water potential at wilting point, or turgor loss point (henceforth π_{tlp}). This functional trait is a good predictor of tree species distribution relative to water supply [8]. The seasonal osmotic adjustment of π_{tlp} contributes to leaf drought tolerance and has been found worldwide in plants [9], and, to a limited extent, in tropical rainforest trees [10,11]. We hypothesized that if lianas are less drought tolerant than trees, as suggested by their greater xylem vulnerability, they should have a less negative π_{tlp}, but they should have a larger osmotic adjustment to achieve sustained growth under dry conditions, which would be

consistent with their overall greater plasticity [12]. To test this hypothesis, we conducted measurements of π_{tlp} for co-occurring trees (n=247) and lianas (n=57) in an Amazonian forest both during the dry and the wet season.

Material and methods

Field measurements were conducted at the Nouragues Ecological Research Station in French Guiana, located 120 km south of Cayenne within an undisturbed forest (4°05' N, 52°40' W). This forest receives c.a. 3000 mm/yr rainfall, with a long wet season from December to July, often interrupted by a short dry period in March. The long dry season (< 100 mm/mo) lasts 2-3 mo, from the end of August to the end November. Lianas have been reported to increase in abundance and productivity at this site [13], and a liana-infested forest formation has encroached [14].

Data were collected in September 2012, May 2014 and September 2015. The cumulative rainfall one month prior the ending date of each sampling session was calculated from half-hourly data (Campbell Scientific SBS500, Shepshed, Leicestershire, UK). In 2012, cumulative rainfall was 21 mm; in 2014, 265 mm; and in 2015, 78 mm (Fig. 1b). Thus, the 2012 and 2015 sampling periods were considered as dry and the 2014 as wet, with the 2012 sampling the driest.

In 2012, we sampled 165 trees of 71 species spanning a wide gradient of ecological strategies. In 2014 and 2015, we sampled 32 and 50 individuals respectively. During the three sessions, we sampled 7, 42 and 8 lianas respectively. Liana taxonomy was resolved using DNA barcoding of leaf samples based on *rbc*L and *mat*K plastid DNA gene regions amplified using classic protocols [15]. Our liana sampling included more than 11 families, the two most represented being Fabaceae and Bignoniaceae (n=10 each). In 2012 and 2015, sampling was restricted to canopy lianas. In 2014, lianas climbing on canopy trees (n=14) and growing in open gaps (n=28) were both sampled. Small branches were collected by climbing the trees using the single-rope technique. π_{tlp} was measured using a previously published field protocol [16]. Briefly, a vapour pressure osmometer (Vapro 5520, Wescor, Logan, UT) is used to measure the osmotic potential at full hydration, which is converted into π_{tlp} using a physical calibration relationship, which was validated at our site [10].

First, we tested the difference in mean π_{tlp} between canopy and gap lianas in the 2014

sampling using a t-test. We then tested for the effect of water availability and growth form on log-transformed π_{tlp} using a two-way ANOVA, with sampling session and form as fixed factors. Post-hoc comparisons were further explored using t-tests or Mann-Whitney-Wilcoxon tests, as appropriate. All statistical analyses were conducted using the R software [17]. Considering our liana and tree unbalanced sampling, test prerequisites of normality and homoscedasticity were thoroughly checked using Shapiro-Wilk and Bartlett tests respectively.

Results

Canopy and gap lianas did not significantly differ in their π_{tlp} (P=0.07), they were thus grouped for subsequent analyses. Both season and growth form significantly influenced π_{tlp} (P<0.001), and the interaction term was also significant (P=0.05). Lianas had a less negative π_{tlp} than trees during the 2014 wet season (P<0.001, mean ± se= -1.59 ± 0.04 MPa versus -1.89 ± 0.05 MPa respectively; Fig. 1), but the difference was not significant during either the 2015 mild dry sampling session (P=0.16, mean ± SE= -1.70 ± 0.07 MPa versus -1.88 ± 0.06 MPa) and the 2012 drier sampling session (P=0.61, mean ± SE= -2.02 ± 0.14 MPa versus -2.01 ± 0.02 MPa).

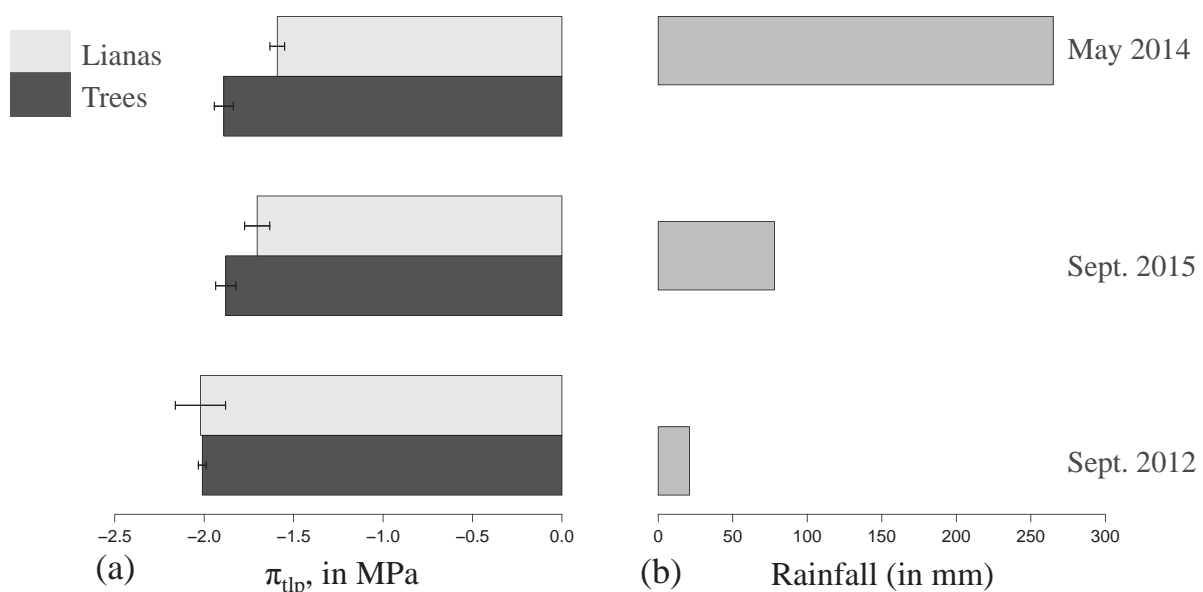**Fig. 1.** (a) Leaf water potential at wilting point (mean ± se, π_{tlp}, in MPa) across growth form and water availability, illustrated in (b) by the cumulative rainfall one month prior the ending date of each sampling session (in mm).

Discussion

Lianas sampled in a tropical rainforest showed a stronger osmotic adjustment than trees during the dry season. Liana leaves were less drought-tolerant than trees in the wet season, but had similar drought tolerances during the dry season.

In the absence of osmotic adjustment, turgor in developing cells declines with water potential. The water potential may be sustained by access to deep water or strong stomatal control under drying conditions, and osmotic adjustment also contributes to turgor maintenance, a critical prerequisite for growth [18]. All these mechanisms would contribute to a liana growth advantage. Previous studies have mainly concentrated on growth limitation due to limited carbon, whereas evidence is mounting that dry season tree growth is not carbon-limited but constrained by turgor-mediated sink activity [19,20]. Anatomically, lianas are exceptionally plastic and resilient. They tend to have more stem parenchyma tissue, especially in contact with vessels [12], which constitute a major storage compartment for non-structural carbon (NSC) [21]. NSC is critical in maintaining the leaf osmotic regulation, and turgor and long-distance vascular integrity in xylem and phloem [20].

Focusing on trees exclusively, Binks *et al.* [11] did not find an osmotic adjustment in π_{tlp} during the dry season in an eastern Amazonian site. However, they did detect an adjustment under stronger water stress induced by artificially excluding throughfall. Based on the finding of stronger osmotic adjustment by lianas shown here during a seasonal drought, we hypothesize that under more intense water stress, lianas would be enabled to equal or outperform trees in drought tolerance. In contrast to these findings, Zhu and Cao [22] found a stronger osmotic adjustment in trees than in lianas in a seasonal tropical rainforest in China. If our results are confirmed at other sites, we predict a lower increase in NSC storage in lianas than observed in co-occurring trees during the dry season because of sink activity limitation [23].

Our study suggests a stronger osmotic adjustment in lianas than in co-occurring trees during the dry season. This provides a mechanism to explain the ability of lianas to maintain growth alongside or exceeding that of trees in the dry season. Future studies should compare π_{tlp} adjustment within given species and seek to simultaneously measure NSC concentration, water balance, C assimilation and growth on co-occurring trees and lianas. Integrated understanding of the responses of hydraulic and plant-level carbon dynamics for lianas and trees is critical for improved prediction of tropical forest responses to climate change.

Acknowledgments

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Seasonal response of tree water transport in a rainforest is revealed by leaf water potential at turgor loss point

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Chapter outline

Chapters 2 to 4 suggest that the leaf water potential at turgor loss point (π_{tlp}) may be a good candidate to help parameterize plant responses to drought in vegetation models. In this **Chapter 5,** the link between π_{tlp} values and whole plant response to drying conditions is explored. Diverse tree sensitivities to drying conditions in the field, as measured by sap flow variation of mature trees during a marked dry season, are investigated and compared to their contrasting π_{tlp} values. As sap flow variation includes both leaf and stem responses to drought, and to further explore the integration of drought-tolerance at the whole plant scale, π_{tlp} values and values of xylem water potential at 50% loss of conductivity (P_{50}) are also compared in a compilation of tropical plant species.

Abstract

The response of vegetation to drought and its diversity remain poorly documented and this hampers our ability to make informed predictions under the predicted increase in drought frequency.

Here we examined to what extent a drought tolerance leaf-level trait, the leaf water potential at turgor loss point (π_{tlp}), may contribute to explain whole-tree water transport decrease as soil dries during a marked dry season in an Amazonian forest. We continuously measured sapflow density on 22 mature trees and estimated their sensitivity to soil drought (S) as the strength of the relationship between soil water content and sapflow density after removing the effect of atmospheric demand. We measured π_{tlp} as well as the leaf predawn water potential (Ψ_{pd}) on the same trees at the beginning of the dry period. We also compared π_{tlp} and P_{50} for a compilation of tropical forest trees (n=95 pairs of trait values).

Sampled trees exhibited a range of S values, which were correlated with π_{tlp} (Spearman test: P<0.01, ρ=0.69). Trees that exhibited more drought-tolerant leaves, as revealed by a more negative π_{tlp}, tended to better maintain plant water transport. By contrast, Ψ_{pd} or tree size did not explain any variability in S in our study. π_{tlp} and P_{50} were positively correlated in our compilation (P=0.001, R^2=0.11) and π_{tlp} was generally less negative than P_{50}, indicating that leaf turgor loss generally precedes widespread xylem cavitation, hence would be a good proxy for decreasing performance under droughted conditions.

We infer that the measurement of π_{tlp} could be an efficient and rapid way of quantifying the slowdown in water uptake during regular dry seasons and help define whole plant behaviour along continuum of strategies of responses to drought.

Key-words: tropical trees, wilting point, sap flow, water transport, Amazonia, drought tolerance, functional trait.

Introduction

Over the past decades, massive drought events have impaired forest ecosystem function and induced tree mortality worldwide (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013). This has raised awareness of the vulnerability of forests, which shelter important stores of biodiversity and carbon globally (Bonan 2008; Pan *et al.* 2011). In particular, Amazonia's important carbon sink transiently shifted to a source because of a drought-induced decrease in tree growth and increase in tree mortality (Feldpausch *et al.* 2016). Some taxa and larger trees appeared particularly vulnerable (Nepstad *et al.* 2007; Phillips *et al.* 2009; da Costa *et al.* 2010), and drought-induced floristic shifts have already been observed in tropical forests (Phillips *et al.* 2010; Fauset *et al.* 2012; Butt *et al.* 2014; Martínez-Vilalta & Lloret 2016). Drought intensity and frequency have been predicted to increase in the future (Dai 2013; Touma *et al.* 2015). However, the response of vegetation to drought and its diversity remain poorly documented and this hampers our ability to make informed predictions (Galbraith *et al.* 2010; Powell *et al.* 2013; Medlyn *et al.* 2016).

Plant response to drought results from a complex interplay of mechanisms operating across scales within the plant (Hsiao 1973; Hartmann *et al.* 2015; Fatichi, Pappas & Ivanov 2016; Corlett 2016). As the soil dries, plant water transport decreases due to more negative plant water potentials that induce a reduction in the hydraulic conductances along the water pathway. Control of the water column tension through stomatal closure and reduced water loss may prevent xylem runaway cavitation and irreversible hydraulic failure (Jones & Sutherland 1991; Sperry, Alder & Eastlack 1993). However stomatal closure is at the cost of carbon assimilation (McDowell *et al.* 2008). This led to the classification of plants into isohydric and anisohydric behaviours (Tardieu & Simonneau 1998). Isohydric plants typically adjust their stomatal opening so as to keep a safe water state at the cost of carbon assimilation; in contrast anisohydric plants maintain assimilation and their hydric state tracks environment fluctuations, at the risk of irreversible tissue damage. This classification was applied to ecosystems composed of few codominant species with contrasting strategies (eg. piñon–juniper woodland; McDowell *et al.* 2008; West *et al.* 2008).

However species-rich communities shelter a continuum of strategies of responses to drought (Martínez-Vilalta *et al.* 2014; Klein 2014; Skelton, West & Dawson 2015) involving various structures and mechanisms such as xylem resistance to cavitation, stomatal closure, deep root system, deciduous leaf habit, stem capacitance or photosynthetic stems (eg. Meinzer

et al. 2009; West *et al.* 2012; Delzon 2015; Pivovaroff *et al.* 2016). Which relevant traits underlying plant performance and survival under drought should be used in vegetation models still remains one of the major controversies in plant hydraulics (Sack *et al.* 2016). Here we report on a field study and examine to what extent a drought tolerance leaf-level trait may contribute to explain whole-tree water transport decreases as soil dries during a marked dry season in an Amazonian forest. An explicit link could help implement more realistic trait-based modelling approaches of plant hydraulic response to drought, using a leaf trait that can be relatively rapidly determined in diverse communities.

Different proxies have been proposed to quantify plant tolerance to drought. The xylem water potential at 50% loss of xylem conductivity (P_{50}, in MPa), which quantifies xylem vulnerability to cavitation, is thought to be a good predictor of drought-related tree mortality (Anderegg *et al.* 2016) and to species distributions relative to water supply (Maherali, Pockman & Jackson 2004; Choat *et al.* 2012). However, measuring xylem conductance and P_{50} is challenging on tropical tree species as they often have long vessels that can induce measurement artefacts (Martin-StPaul *et al.* 2014; Torres-Ruiz *et al.* 2014; Delzon 2015). A recent compilation of 480 P_{50} values worldwide did not contain a single Amazonian tree species (Choat *et al.* 2012). Besides, hydraulic failure is a rare event in trees (Delzon & Cochard 2014) and P_{50} may not well inform on the variety of plant responses under incipient and continuous drying conditions well before cavitation occurs.

The first noticeable plant response under water stress is a reduction of turgor-driven cell expansion and division, hence a reduction of growth, followed by a reduction of stomatal conductance (Hsiao 1973; Fatichi *et al.* 2016). Turgor decrease has been previously mentioned as critical for the prevention of embolism via its influence on stomatal closure (Sperry & Saliendra 1994; Salleo *et al.* 2001; Cochard *et al.* 2002; Brodribb *et al.* 2003; Martorell *et al.* 2014; Nolf *et al.* 2015). More generally, leaves have been thought to operate as 'expendable safety valve' in order to protect more 'expensive' stem from embolism, a hypothesis known as the hydraulic segmentation hypothesis (Zimmermann 1983; Tyree & Ewers 1991; Tyree & Zimmermann 2002; Pivovaroff, Sack & Santiago 2014). The relative strengths of leaf control and xylem vulnerability to cavitation may be measured based on the time-consuming monitoring of leaf and soil water potentials under dry conditions (eg. Martínez-Vilalta *et al.* 2014) or by direct measurement of vulnerability of stomatal conductance relative to the one of xylem conductance (eg. Skelton *et al.* 2015).

Alternatively, Meinzer *et al.* (2016) recently proposed that the leaf water potential at turgor loss point (henceforth denoted π_{tlp} in MPa) could be a proxy of both species drought-

tolerance and their degree of iso- vs. anisohydry. Plant with a more negative π_{tlp} tend to maintain critical processes, such as leaf conductance and photosynthetic gas exchange under drier conditions (Cheung, Tyree & Dainty 1975; Abrams & Kubiske 1990; Brodribb *et al.* 2003; Bartlett, Scoffoni & Sack 2012b). π_{tlp} was also found strongly correlated with diverse metrics of stringency of stomatal control of leaf water potential across 8 temperate species (Meinzer *et al.* 2016). This leaf-level trait π_{tlp} varies widely across species within communities and biomes (Lenz, Wright & Westoby 2006; Maréchaux *et al.* 2015) and explains species distributions relative to water supply within and across biomes (Lenz *et al.* 2006; Baltzer *et al.* 2008; Bartlett *et al.* 2012b) as well as community assemblages (Bartlett *et al.* 2015).

We measured sapflow density on mature trees in an Amazonian rainforest during a marked dry season, and measured π_{tlp} on the same trees. We also measured their leaf predawn water potential (Ψ_{pd}, in MPa), a proxy of water availability in the root zone. Finally, we compared π_{tlp} and P_{50} for a compilation of tropical forest trees, in order to explore coordination of whole plant response and tolerance to drought (Reich 2014). We hypothesized that (i) trees with a more negative π_{tlp} are less sensitive to soil drying, and tend to better sustain sap flux density; (ii) trees with less negative Ψ_{pd} have a better access to soil water, and thus also better sustain sap flux density; (iii) larger trees are more sensitive to soil drought because of stronger hydraulic constraints, and thus are less able to sustain sap flow density; (iv) π_{tlp} and P_{50} are positively correlated since drought tolerance should be coordinated in leaves and sapwood.

Material and Methods

Study sites and sampling

Field measurements were conducted at the Nouragues Ecological Research Station in French Guiana. It is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05' N, 52°40' W; Bongers *et al.* 2001). The site receives ca. 3000 mm/yr rainfall, with significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. A long wet season lasts from December to July, often interrupted by a short dry period in March. The long dry season lasts from the end of August to November with 2-3 months with precipitation <100 mm/mo (Bongers *et al.* 2001). Data were collected in a 12-ha permanent forest plot on clay-sand soil (Petit Plateau) where

all trees ≥10 cm diameter at breast height (DBH) were identified. Twenty-two mature canopy trees of 10 species known to present contrasting leaf drought tolerance (Maréchaux *et al.* 2015) were sampled during the dry season 2015 (Table 1).

Table 1. Characteristics of the 22 trees for which sapflow density was measured during a dry season. Dbh, diameter at breast height (in mm); leaf fall indicates if the tree shed a significant amount of leaves during the sampling period; mean D_s, sapflow density averaged across the first 10 days (beginning) and the last ten days (end) of the sampling period, in kg/dm^2/day; π_{tlp}, leaf water potential at turgor loss point, in MPa. For tree DG4, we do not provide mean D_s across the first 10 days since leaf fall occurred during that period. π_{tlp} values are not reported for *Qualea* species because the method of determination is not robust for this genus (Maréchaux *et al.* 2016).

Species	Tree code	Dbh (mm)	Leaf fall	Mean D_s (kg/dm^2/day)		π_{tlp} (MPa)
				Beginning	End	
Dicorynia guianensis	DG1	460	N	14.2	8.8	-1.53
Dicorynia guianensis	DG2	622	N	13.6	7.6	-1.62
Dicorynia guianensis	DG3	661	N	11.8	9.3	-1.60
Dicorynia guianensis	DG4	598	Y	-	10.7	-1.70
Dicorynia guianensis	DG5	761	Y	11.4	7.9	-1.60
Vouacapoua americana	VA1	662	Y	11.7	11.8	-2.19
Qualea rosea	QR1	232	N	8.5	9.9	-
Qualea rosea	QR2	636	N	11.1	4.2	-
Qualea rosea	QR3	515	N	3.4	3.9	-
Qualea c.f. tricolor	QT1	715	N	6.4	5.1	-1.66
Qualea c.f. tricolor	QT2	907	N	8.5	8.5	-1.81
Licania alba	LA1	417	N	6.9	6.4	-1.92
Licania alba	LA2	326	N	4.4	4.1	-2.00
Licania alba	LA3	390	N	9.7	8.0	-1.91
Licania rodriguesii	LR1	530	N	10.3	9.8	-2.01
Lecythis poiteaui	LP1	414	N	10.5	10.6	-2.93
Lecythis poiteaui	LP2	657	Y	3.1	1.2	-2.54
Eschweilera coriacea	EC1	337	N	6.3	5.9	-1.61
Eschweilera coriacea	EC2	283	N	7.1	5.7	-1.59
Eschweilera coriacea	EC3	353	N	5.3	4.6	-1.80
Goupia glabra	GG1	351	N	4.1	3.4	-2.06
Sextonia rubra	SR1	859	N	2.9	2.6	-1.61

Plant hydraulic traits

Leaf water potential at predawn (Ψ_{pd}, in MPa) and at turgor loss point (π_{tlp} in MPa) were measured on each tree at the beginning of the dry season (between calendar days 251 and 257). Small top-canopy branches were collected by climbing the trees using the single-rope technique (Anderson *et al.* 2015).

Ψ_{pd} was measured on one to three leaves per tree with a Scholander-type pressure chamber (model 1000, PMS Instruments, Corvalis, Oregon, U.S.A.; Boyer & PrometheusWiki contributors 2011) right after sampling, between 5:30 and 7:00 am. In the analyses, Ψ_{pd} was used as a proxy of tree soil water potential and water availability in the root zone (Stahl *et al.* 2013b). In doing so, we assumed that plant and soil water potentials equilibrate overnight (Fisher *et al.* 2006; Martínez-Vilalta *et al.* 2014, but see Donovan, Linton & Richards 2001). π_{tlp} was measured using a rapid method of determination (Bartlett *et al.* 2012a) based on a well-established correlation of π_{tlp} with the leaf osmotic potential at full hydration (Lenz *et al.* 2006; Bartlett *et al.* 2012b), which is measurable with an osmometer (Vapro 5520, Wescor, Logan, UT). This method was further validated on tree species at our site (Maréchaux *et al.* 2016). A detailed protocol of the method is provided elsewhere (Bartlett *et al.* 2012a). π_{tlp} values for individuals of the genus *Qualea* (Vochysiaceae ; species *Qualea rosea* Aubl. and *Qualea c.f. tricolor*) were not used as the method is not valid for leaves that present a dense network of leaf secondary veins (Kikuta & Richter 1992; Maréchaux *et al.* 2016).

Sapflow density

Sap flow density of each tree was continuously measured from day 256 to day 310 (except a few data gap due to battery failure on the field). Measurements were obtained with homemade Granier-type sensors (Granier 1987) as in Stahl *et al.* (2013). These sensors consisted of two probes (20-mm long×2mm in diameter) that were inserted radially into the outer xylem. The upper probe was heated and the lower one (reference) was not. The two holes for the probes were drilled into the trunk 15 cm apart, ca. 1.5 m above the ground. Sap flow density was inferred from the measured difference in temperature between the heated and the reference probe as in Granier (1987). We covered the probes with an aluminium-coated sheet of plastic bubble-wrap in order to reduce any potential error caused by the sun heating the trunk. Heat flux density was logged every 30 sec in a datalogger (Campbell Scientific CR23X, Shepshed, Leicestershire, UK) and averaged every 30 min. We then summed these values for each day and henceforth used the daily sap flow density (D_s, kg/dm^2/day) to investigate seasonal variations in whole plant water transport.

Environmental data

Incoming irradiance, temperature, relative humidity, wind speed and direction, and rainfall

were measured at the site every half-hour during the whole year using a micrometeorological station (Hukseflux SR11, Delft, Netherlands; Vaisala HMP155A, Vantaa, Finland; Yound, Wind monitor 05103, Traverse City, Michigan, USA; Campbell Scientific SBS500, Shepshed, Leicestershire, UK) and a datalogger (Campbell Scientific CR1000, Shepshed, Leicestershire, UK). Potential evapotranspiration (PET, in mm) was computed with the Penman–Monteith equation (Allen *et al.* 1998).

Soil water content variation was measured using a time-domain reflectometry probe (Campbell Scientific CR1000, Shepshed, Leicestershire, UK) at 20cm soil depth. Missing soil water content data (Fig. 1) were gap-filled based on look-up tables established on recorded values. Soil water content data were averaged daily and standardized relative to the value measured at field capacity, estimated when excess water from abundant rain events has drained away.
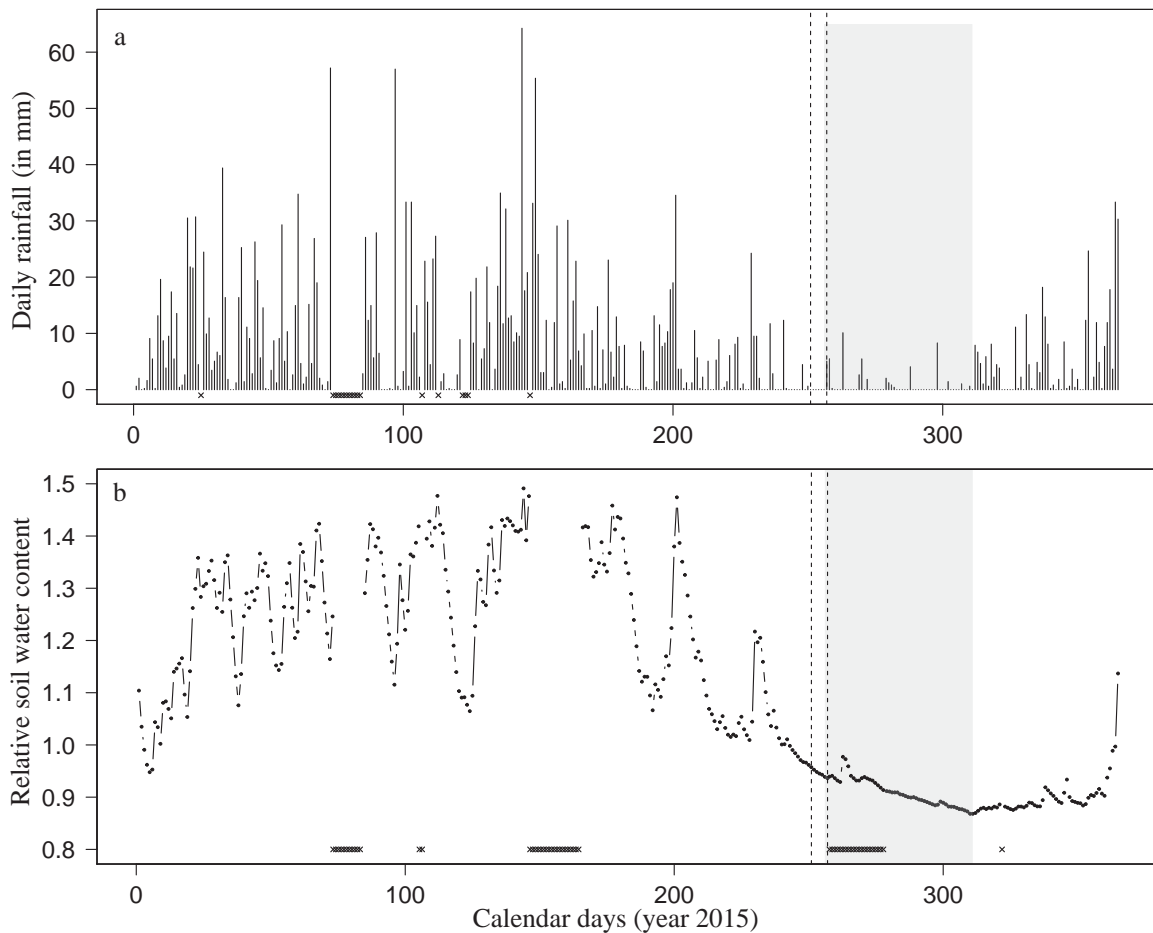
Fig. 1. Variation in (a) daily rainfall (in mm) and (b) relative soil water content for 2015. Dotted black lines: period during which leaf water potentials were measured; shaded grey band: period during which sapflow density was continuously measured and half-hourly logged. Daily averaged soil water content was computed from a time-domain reflectometry probe set at 20 cm depth and measured relative to the value measured at field capacity, estimated when excess water from abundant rain events has drained away. Black crosses: gap-filled values during the sampling period.

Data analysis

We investigated relationships between π_{tlp}, Ψ_{pd} and diameter at breast height (dbh, in mm; Table 1) across trees using non-parametric Spearman tests. For each tree, we quantified the sensitivity of daily sapflow density to decreasing soil water content (S). To this end, we first computed the residuals of the regression between tree sapflow density and potential evapotranspiration ($D_s \sim PET$), henceforth $D_{s/PET}$. These residuals quantify tree water transport after accounting for the variability due to atmospheric demand. The sensitivity S was then defined as the R^2 of the linear regression between $D_{s/PET}$ and relative soil water content. Hence, S is the sensitivity to soil water content of tree water transport once atmospheric demand has been accounted for. We tested if tree π_{tlp}, Ψ_{pd} or dbh explained S variability across individuals using Spearman tests.

Meta-analysis

In order to further investigate responses to drought at plant scale, we compiled a dataset with both leaf water potential at turgor loss point (π_{tlp}, in MPa) and water potential at which 50% of xylem conductivity is lost (P_{50}, in MPa) by searching the literature in ISI Web of Knowledge and Google Scholar. We limited our search to sites with mean annual rainfall above 1500mm (moist tropical rain forests). In order to reduce variability due to environmental plasticity, which is known to be common for both traits (Bartlett *et al.* 2014; Anderegg 2015), pairs of π_{tlp} and P_{50} values were included only if they had been measured within the same study, at the same site and during the same season. In total we compiled 95 pairs of π_{tlp} and P_{50} values corresponding to unique combinations of species, site and season (see Appendix).

We explored the relationship between π_{tlp} and P_{50} by fitting a standard major axis (SMA) linear function on log-transformed data (Warton *et al.* 2012). Our compilation includes values of P_{50} that were inferred using different methods (benchtop dehydration method: n=48; air-injection method: n=47), whose consistency has been questioned (Cochard *et al.* 2013; Torres-Ruiz *et al.* 2014). We thus tested if the relationship between π_{tlp} and P_{50} was consistent across methods. We also checked whether the relationship was biased toward a few sites disproportionately represented in our compilation. Finally we investigated the distribution of the safety margin computed as the difference betwen π_{tlp} and P_{50}.

All statistical analyses were conducted using the R software (R Core Team 2013) and the MASS (Venables & Ripley 2002) and SMATR (Warton *et al.* 2012) packages.
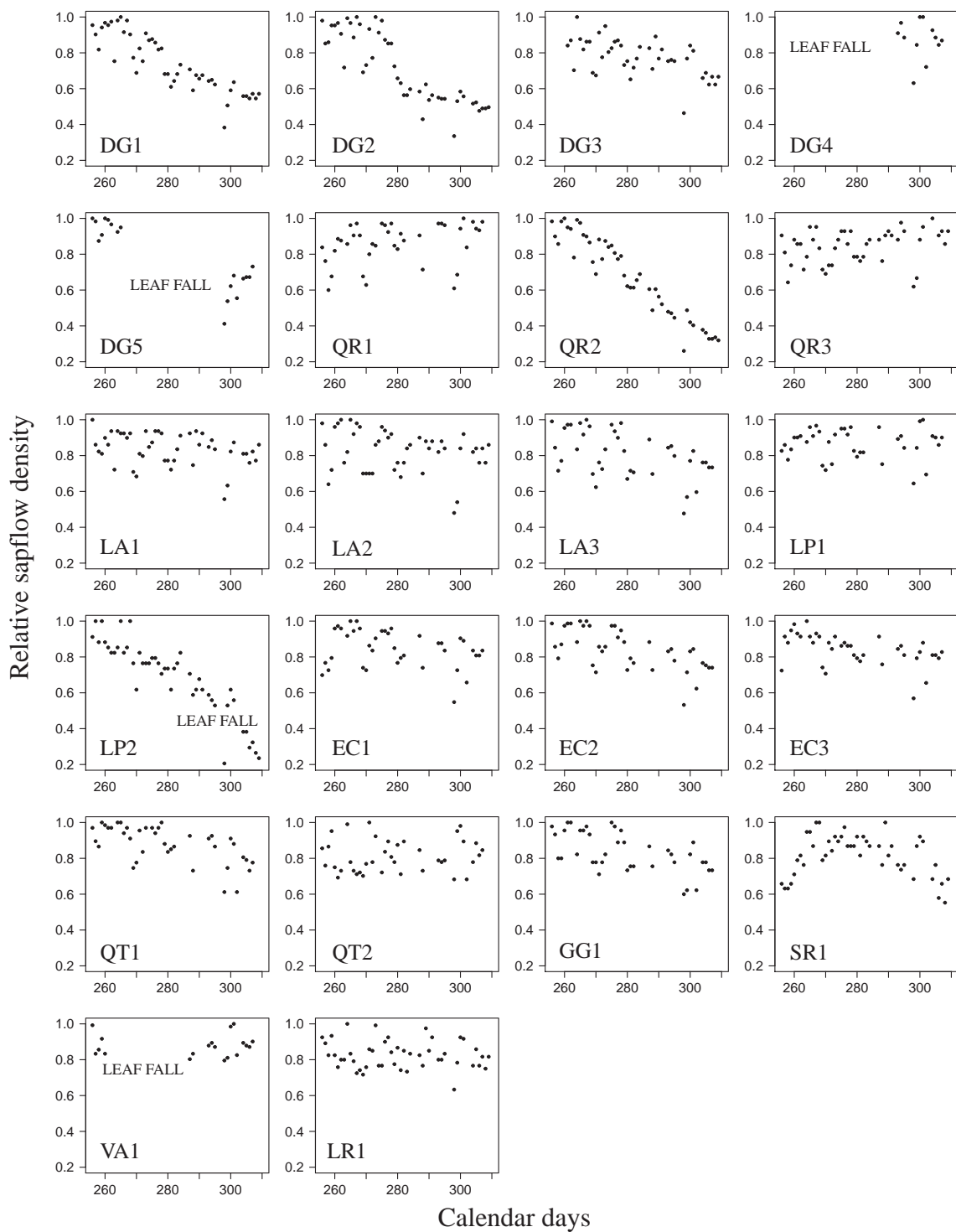
Fig. 2. Variation in daily sapflow density for the 22 sampled individuals. For each tree, sapflow density is given relative to its maximum during the sampling period. See Table 1 for tree codes. Periods of significant leaf shedding are specified (leaf fall, see maintext).

Results

Determinants of tree sapflow density decrease during a drought

During the sapflow measurement period (55 days), rainfall was 50.5 mm (Fig. 1a), and rainfall events were limited, if present, and were unlikely to refill the water table, with only 16 days with positive rainfall below 10 mm. Soil water content showed a marked decrease during this period, in comparison to the rest of the year (Fig. 1b). During this period, two *Dicorynia guianensis* Amshoff (Fabaceae) trees, one *Lecythis poiteaui* O.Berg (Lecythidaceae), and one *Vouacapoua americana* Aubl. (Fabaceae) shed most of their leaves. Their sapflow declined quickly until reaching negligible flow, until new leaf flushed (Fig. 2). Deciduousness at our site appeared unrelated to leaf drought tolerance, as trees that lost their leaves spanned the whole range of π_{tlp} values in our dataset (Table 1). Note also that some trees of the same species did not shed their leaves. The four deciduous individuals were removed from subsequent analyses using S.

The other trees presented contrasting trends in sapflow density, with a reduction of sapflow density relative to their maximum of 26-67% during the period (Fig. 2). The explanatory power of potential evapotranspiration (PET) for tree daily sapflow density (D_s) was quite variable (R^2 of D_s~PET spanned from 0.02 to 0.47). Sensitivity to soil water content S was also quite variable (from 0.0 to 0.85) and was positively correlated with tree π_{tlp} (Spearman test, P<0.01, ρ=0.69, n=13 individuals; Fig. 3), but not with tree Ψ_{pd} (Spearman test, P=0.25) or dbh (Spearman test, P=0.88). We found that π_{tlp} ranged from -2.93 to -1.53 MPa and Ψ_{pd} from -0.15 to -0.45 MPa. π_{tlp}, Ψ_{pd} and dbh were not correlated with each other across trees (Spearman test, all P>0.55).
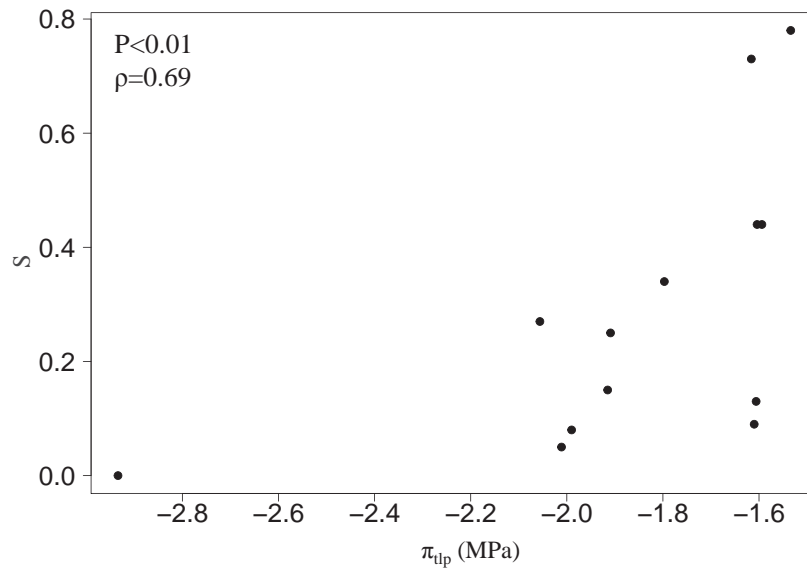
Fig. 3. Correlation between the sensitivity of tree sapflow density to decreasing soil water content (S) and tree leaf water potential at turgor loss point (π_{tlp}, in MPa). S was quantified for each tree as the R^2 of the linear regression between the residuals of the regression between tree sapflow density and potential evapotranspiration ($D_s \sim PET$) on the one hand, and relative soil water content on the other hand.

Relationship between π_{tlp} and P_{50}

π_{tlp} and P_{50} were weakly positively related (SMA: P=0.001, R^2=0.11, n=95 species×site×season; Fig. 4a). Slopes did not differ when restricting the relationship to each method of P_{50} determination (P=0.37), but the relation was not significant for the dataset including air-injection method only (n=47, P=0.92) and was stronger when including benchtop dehydration only (n=48, P<10^{-4}, R^2=0.30). The positive and weak relationship did not depend on the over-representation of some sites in our dataset. The safety margin between π_{tlp} and P_{50} was positive in 55% of the cases and on average (one-tailed t-test: P=0.003, averaged safety margin=0.24 MPa). However it varied from -1.12 MPa to 3.11 MPa and tended to increase with decreasing (more negative) P_{50} values (Fig. 4b). Consistently, the slope of the relationship between π_{tlp} and P_{50} was significantly larger than 1 (P<10^{-7}, 95%-confidence interval=[1.45; 2.13], Fig. 4a).
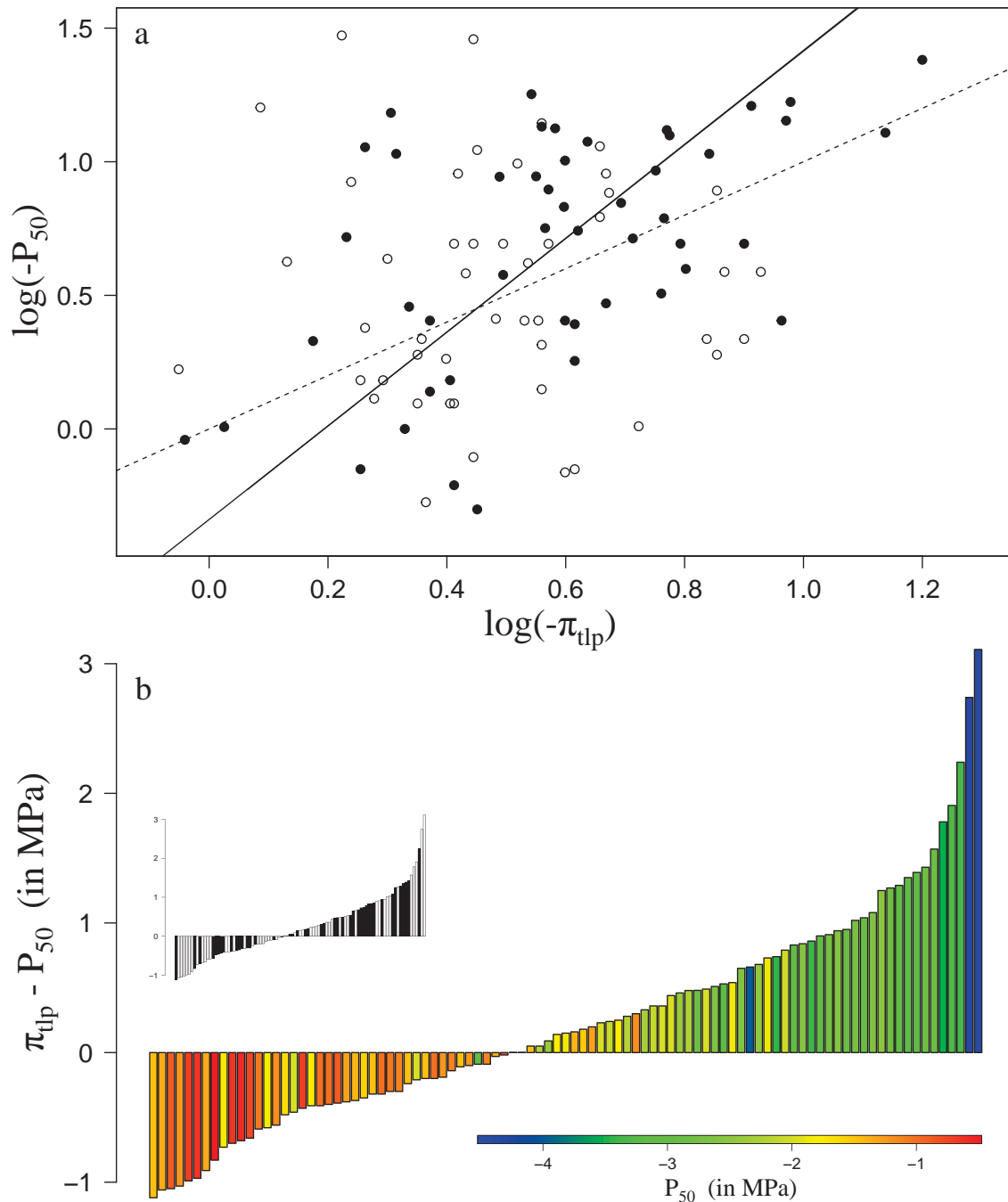
Fig. 4. (a) Relationship between leaf water potential at turgor loss point (π_{tlp}, in MPa) and xylem water potential at 50% loss of xylem conductivity (P_{50}, in MPa). Black line shows the standard major axis fitted on log-transformed data (n=95 species×site×season, P=0.001, R^2=0.11) and dashed line shows the 1:1 line. (b) Distribution of safety margins between π_{tlp} and P_{50} ranked by increasing order. Continuous color scale shows corresponding P_{50} values. Black and white colors in (a) and inset in (b) correspond respectively to benchtop dehydration (n=48) and air-injection methods (n=47) of P_{50} determination.

Discussion

Trees studied at our site exhibited a range of hydraulic responses under increasing soil water stress during a dry season. This is in agreement with previous reports in a nearby site, where Stahl *et al.* (2013a) found gas exchange and transpiration to strongly decrease as soil water content decreased during a dry season for some trees, but not for other co-occuring trees. Our major result is that the leaf-level drought tolerance trait π_{tlp} correlated with the sensitivity of sapflow density to the increasing soil drought. Trees that exhibited more drought-tolerant leaves, as revealed by a more negative π_{tlp}, tended to better maintain plant water transport, hence transpiration and whole plant functioning along the dry season than trees with less negative π_{tlp}. So we infer that the measurement of π_{tlp} could be an efficient and rapid way of quantifying not only the susceptibility of trees to major drought events, but also the slowdown in water uptake during regular dry seasons. This is in agreement with reported link between stomatal closure dynamics and π_{tlp} (Brodribb *et al.* 2003; Hao *et al.* 2010; Klein 2014). Eventually π_{tlp} may help define whole plant behaviour along continuum of strategies of responses to drought (Martínez-Vilalta *et al.* 2014; Klein 2014; Skelton *et al.* 2015; Meinzer *et al.* 2016).

In contrast to π_{tlp}, Ψ_{pd} did not explain the variability in tree water transport sensitivity to water stress. However Ψ_{pd} is expected to measure the soil hydraulic status in the root zone. One explanation is that our sampling of leaf predawn water potentials was limited to a period when water stress was not yet strong. The range of Ψ_{pd} across trees was thus small and probably not sufficient to reveal the contrasting abilities of root systems to allow prolonged access to soil water during a drought, as found at a nearby site (Stahl *et al.* 2013a; b). Consequently our analysis may not be appropriate to quantify the effect of soil-to-root water supply on plant water use under droughted conditions (Fisher *et al.* 2007). The absence of coordination of Ψ_{pd} and π_{tlp} is however in agreement with other studies (Lenz *et al.* 2006; Choat, Sack & Holbrook 2007; Pivovaroff *et al.* 2016), that suggested that plant performance under droughts actually result from diverse mechanisms that can vary independently among individuals.

Also, tree size, as inferred from diameter at breast height, was not correlated with π_{tlp} or Ψ_{pd}, in agreement with previous reports at our site or nearby (Stahl *et al.* 2013b; Maréchaux *et al.* 2016). Higher vulnerability of larger trees have been reported under artificial and natural extreme drought events in Amazonia (Nepstad *et al.* 2007; Phillips *et al.*

2009; da Costa *et al.* 2010), which may result from higher xylem vulnerability to cavitation (Rowland *et al.* 2015). However, bigger trees did not show greater water transport sensitivity to soil water stress relative to smaller trees in our sampling during a dry season.

During the study, several trees shed their leaves and produced new leaves. Leaf phenology appeared not directly related to leaf drought tolerance. This is not surprising regarding the reported absence of clear climatic driver of leaf phenology and demography in tropical rainforests (Wright & Cornejo 1990; Reich *et al.* 2004; Chave *et al.* 2010; Wu *et al.* 2016). Leaf phenology may instead be constrained by long-term adaptive strategies (Wright & van Schaik 1994; Wu *et al.* 2016). All deciduous trees in our study belong to species that were previously reported to have a deciduous habit (Loubry 1994; Mori *et al.* 1997), even though some conspecifics also kept their leaves during the period. Overall leaf phenology and demography are poorly understood (Fu *et al.* 2014) despite evidence of its critical role in the seasonality of tropical rainforest ecosystem photosynthesis (Wu *et al.* 2016).

Also, asynchronous leaf development pattern may contribute to the stability and maintenance of diversity and ecosystem functions through temporal niche partitioning (Chesson & Huntly 1997; Sapijanskas *et al.* 2014). The order of magnitude of water transpired by a tree may be estimated by assuming that a typical tree has a sapwood thickness ST of 4 cm, a crude (Stahl *et al.* 2010; Lehnebach *et al.* 2013) but reasonable first assumption (Granier, Huc & Barigah 1996). From this, the sapwood area is calculated from the formula $\pi \times ST \times (dbh - ST)$. At the end of our sampling period (Table 1), the total amount of water transpired daily was only 15% lower than at the beginning of the period. Individual tree contributions ranged from 0 to 103 l/day at the start of the sampling, and 9 to 92 l/day at the end.

The positive relationship we found between π_{tlp} and P_{50} in our compilation suggests that π_{tlp} informs whole plant drought-tolerance. Such a coordination of drought-tolerance among the different plant organs sounds logical from a whole-plant optimization standpoint (Reich 2014). It is also in agreement with site-specific reports (Brodribb *et al.* 2003; Choat *et al.* 2007; Fu *et al.* 2012; Zolfaghar *et al.* 2015) and more generally with the reported coordination between stem and leaf hydraulic functions (Sack *et al.* 2003; Meinzer *et al.* 2008, 2009; Manzoni 2014; Klein 2014; Nolf *et al.* 2015; Pivovaroff *et al.* 2016). We found that π_{tlp} was generally less negative than P_{50}, indicating that leaf turgor loss generally precedes widespread xylem cavitation, hence π_{tlp} would be a good proxy of decreasing hydraulic performance under droughted conditions. This is in agreement with the hydraulic segmentation hypothesis (Zimmermann 1983; Tyree & Ewers 1991; Tyree & Zimmermann

2002; Pivovaroff *et al.* 2014). This may be even more true considering that our analysis may have underestimated the effective safety margin between leaf turgor loss and critical xylem cavitation because in angiosperm species the 88% loss of conductivity (P_{88}) rather than P_{50} better corresponds to the threshold for xylem recovery failure (Urli *et al.* 2013).

The margin between between π_{tlp} and P_{50} was found to decrease with increasing vulnerability to cavitation (see also Meinzer *et al.* 2009; Klein 2014). Since anisohydric species exert little stomatal control and thus operate with narrower hydraulic safety margins than isohydric species, they should be more predisposed to hydraulic failure (McDowell *et al.* 2008). They however appeared to experience lower mortality under droughts (McDowell *et al.* 2008). Our results here show that the safety margin between leaf control and xylem cavitation may actually increase with decreasing P_{50} and π_{tlp}, hence with the ability to tolerate more negative water potentials. This is in agreement with recent findings that show that a typical anisohydric species showed very little embolism due to its conservative leaf stomatal regulation before the embolism entry point. By contrast, a co-occuring typical isohydric species exhibited chronic embolism despite less variable plant water potentials (Garcia-Forner *et al.* 2016; see also Quero *et al.* 2011; but see Skelton *et al.* 2015). This challenges the idea that curves of leaf water potential under drying conditions allow on their own to identify mechanisms of drought-induced mortality (McDowell *et al.* 2008; Hartmann 2015; Rowland *et al.* 2015). Instead, tolerance thresholds may be considered to describe response and vulnerability to drought (Martínez-Vilalta *et al.* 2014; Skelton *et al.* 2015).

Overall the fact that a leaf-level trait informs a significant part of plant hydraulic response under water stress opens interesting perspectives of vegetation modelling. Soil water availability was found to be the main climatic driver of tree growth variability in a closeby site (Wagner *et al.* 2012), but the latter was poorly explained by commonly measured traits (Wagner *et al.* 2014). In addition to our results, this calls for a further trait-based exploration of the determinants of tree growth response that include hydraulic and drought tolerance trait such as π_{tlp} (Christoffersen *et al.* 2014; Pappas, Fatichi & Burlando 2016; Xu *et al.* 2016). We suggest this would improve model performance and help shifting from carbon source to sink-driven plant modelling approach (Fatichi, Leuzinger & Körner 2014; Körner 2015).

Acknowledgments

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GENERAL DISCUSSION

I. Synthesis

A great part of the uncertainty in our current understanding and projections of carbon cycle, hence of climate and its impacts, lies in vegetation (Moorcroft 2006; Fisher *et al.* 2014). The development of robust dynamic vegetation models has been hindered by several challenges and constraints. Incomplete knowledge of physiological mechanisms underlying vegetation response to various biotic and abiotic perturbations prevents a realistic representation of some processes, which are however critical for a full understanding of these phenomena. Hence, despite observations of forest vulnerability to drought and predictions of increasing drought events, vegetation response to drought is still represented in a crude way leading to large data-model discrepancies (Powell *et al.* 2013; Joetzjer *et al.* 2014; Meir, Mencuccini & Dewar 2015a). Also, both computational and data limitations have long constrained models to adopt a coarse-grained representation of vegetation structure, biodiversity, and environmental heterogeneity. This has limited models' ability to represent ecosystem properties accurately. Even though these are often investigated at stand to global scales (e.g. biomass), they depend *in fine* on individual processes (e.g. stem mortality, Johnson *et al.* 2016) and on the diversity of ecological strategies (Poorter *et al.* 2015).

Next-generation vegetation models should thus better integrate both individual structure (Moorcroft, Hurtt & Pacala 2001; Grimm & Berger 2016) and specific and functional diversity (Loreau 2010; Mokany *et al.* 2016) to improve their predictive power in a changing world and for a community of decision makers and stakeholders in high demand of predictions (Moorcroft 2006; Purves & Pacala 2008; Mouquet *et al.* 2015). The high biodiversity of tropical forests, their disproportionate role in global biogeochemical cycles, together with their recognized vulnerability to direct and indirect anthropogenic perturbations, amplify both the difficulties and the importance of this research challenge. The development of processes-based knowledge and of our predictive ability requires transdisciplinary and complementary approaches, in which field investigation and experimental measurements feed model development (Medlyn *et al.* 2015), while modelling exercises guide the empirical development of knowledge (Fisher *et al.* 2006; Medlyn *et al.* 2016).

In the first chapter of this thesis a new individual-based and spatially explicit forest model is described and parameterized for an Amazonian rainforest. TROLL uses a finer-

grained representation of space and individuals than global vegetation models and gap models usually do, while integrating processes underlying plant responses to environment in a mechanistic way. These physiological processes that controlled tree birth, growth, death and reproduction are modelled with species-specific parameters. TROLL thus keeps track of species identity and dynamics, taking advantage of increasingly available information on plant functional traits (Kattge *et al.* 2011). It thus allows to jointly simulate the carbon uptake and allocation and biodiversity composition and presents desirable attributes for an integrated model of biodiversity and ecosystem function (Table 1, Mokany *et al.* 2016). The model yields outputs that are comparable to both field inventory data that provide information on community demography and composition at the individual and species scales, and ecosystem measurements of flux and structure at the stand scale.

Outputs of a simulation of forest regeneration, from bare soil to a 500-year-old mature forest, were in good agreement with data of various types and scales. A sensitivity analysis highlighted the importance of some parameters and processes in shaping ecosystem properties. Limited knowledge we have on some of the parameters, such as those that control carbon allocation or light use efficiency, calls for increased effort in field measurements, or for tests of alternative hypotheses by mean of modelling experiments. TROLL's structure also allowed an exploration of the effects of negative density-dependence, species richness, and species composition on forest dynamics and structure, thus exploring important theoretical questions. It confirmed the importance of density-dependence effects on community biodiversity evenness. Higher species richness tended to enhance ecosystem properties, such as gross primary productivity and aboveground biomass, but this was mostly due to species identity and functional composition rather than species richness per se. It thus further called for care regarding biodiversity representation in models.

Overall, the TROLL model has a code architecture upon which future improvements can be built. Model projections should be based on the inclusion of various changing environmental drivers, especially nutrient and water cycle. This is a needed future improvement for TROLL. Forest response to increasing nutrient deposition and imbalance (Peñuelas *et al.* 2013; Powers *et al.* 2015; Santiago 2015) or drought (Boisier *et al.* 2015; Touma *et al.* 2015) could not be explored. Some of these improvements require a deeper understanding before integration in TROLL. Chapters 2 to 5 of this thesis thus aimed at documenting drought-tolerance and its diversity in Amazonian forests.

Table 1. Essential and desirable attributes of an integrated model of biodiversity composition and ecosystem function, as proposed by Mokany *et al.* (2016), and the degree to which they are currently included or could be integrated in the TROLL model (Chapter 1). ✓: included, ~: potentially included, ×: not included. Adapted from Table 2 in Mokany *et al.* (2016).

Attributes required for an integrated model, proposed by Mokany *et al.* (2016)	In TROLL	Comments, potential TROLL incremental improvements and challenges
Essential		
Spatially explicit	✓	Integration of a spatially explicit belowground space and topography, under development.
Temporally explicit (i.e. dynamic)	✓	
Fine spatial resolution (e.g. $\leq 1 \text{ km}^2$)	✓	
Fine temporal resolution (e.g. ≤ 1 month)	✓	Including the temporal stochasticity of rainfall events might require finer resolution or integration (Laio *et al.* 2001).
Applicable across large extents (regional, continental, global)	~	Upscaling is a forthcoming challenge (see section II-3).
Informed by current patterns in diversity	✓	
Informed by current patterns in structure / function	✓	
Considers important processes at the species level (e.g. physiological tolerances, local colonisation/extinction, dispersal)	✓	Tolerance to water and nutrient limitations to be integrated (see section II-1). Species variation in dispersal ability could be added explicitly from existing knowledge of seed dispersal mode (Hammond *et al.* 1996; Baraloto & Forget 2007).
Considers important ecosystem processes (e.g. photosynthesis, predation/herbivory, growth, disturbance)	✓	Several submodules to be added to close the carbon, nutrient (eg. wood decay, Hérault *et al.* 2010; herbivory, Metcalfe *et al.* 2014) and water cycles (see section II-1).
Considers all the diversity (species) within multiple taxonomic groups	✓	Palms to be added. Lianas could be added (see section II-1-e).
Considers continuous variation in attributes between species	~	Intra-specific variability could be added (see section II-2).
Desirable		
Modest amount of information/parameters required	✓	A few common functional traits are required currently in TROLL, future improvements should seek to keep this number low.
Can be applied to any region or system	✓	Mostly conditioned to the availability of species-specific traits, which is rapidly increasing worldwide (Kattge *et al.* 2011). Future improvements may toughen the constraints.
Easy to apply (e.g. freely available, desktop application)	✓	TROLL source code is available on the GitHub open platform and can be launched from any operating system.
Can explicitly incorporate human management actions	✓	A management (logging scenarios) module is to be added.
Transparent and well documented	✓	A TROLL user guide is being developed (see Appendix A).
Fast run time (even over large regions)	~	Code parallelisation is being implemented to allow faster simulations at regional scales.
Easy to interrogate outputs / projections	~	The development of an R package to allow easy use of TROLL outputs is planned.

In tropical forests, the exploration of drought tolerance traits is limited by methodological issues, since measurements are either prone to artefacts or very time-consuming and impractical on a large number of canopy trees at the community scale. In this thesis, I used and validated a recently developed rapid method of determination of a leaf drought tolerance trait, the leaf water potential at turgor loss point (π_{tlp}; Bartlett, Scoffoni & Sack 2012b; Bartlett *et al.* 2012a Chapter 2-5). This allowed establishing the first community assessment of such a hard drought tolerance trait in an Amazonian forest at the community scale.

This dataset provided insights on the drivers and determinants of π_{tlp}. Within a dataset spanning 165 individuals of 71 species during a dry season, π_{tlp} varied little within species and significantly across species (Chapter 2). A deeper exploration of π_{tlp} variability using additional measurements on 86 individuals of a subset of 9 species at the same site during a wet season (Chapter 3) further confirmed that species identity is the major driver of π_{tlp} variation, whereas season, canopy tree size, and leaf exposure explained little variation. However, π_{tlp} of saplings was only a moderate predictor of π_{tlp} measured on conspecific canopy trees, calling for care when scaling to canopy trees leaf-level drought tolerance measurements based only on saplings and assessing species performance across the entire life cycle (Chapter 3). π_{tlp} showed only a weak or no correlation with other commonly measured plant traits, which precludes the use of soft traits as surrogates and calls for direct measurements of π_{tlp} (Chapter 2).

Some species were clearly more drought tolerant than others (Chapter 2). Furthermore early-successional species tended to exhibit less negative π_{tlp} values than later-successional species (Chapter 3), in agreement with reported coordination of species' drought tolerance and shade tolerance (Markesteijn *et al.* 2011a; b; Reich 2014). Lianas (n=57 measurements) completed this gradient, since these plants are favoured by perturbations and high-light conditions (Schnitzer & Bongers 2011; Ledo & Schnitzer 2014; Santiago, Pasquini & De Guzman 2015), and were also found to have an overall less negative π_{tlp} than trees in our sampling (Chapter 4). However, they showed greater seasonal plasticity in π_{tlp} and reached similar leaf drought tolerance than trees during the dry season. If confirmed, this could pave the way to a new understanding of the reported dry growth season advantage of lianas over trees (Schnitzer 2005; Schnitzer & Bongers 2011). Indeed this liana growth advantage has been advanced to explain the increasing lianas abundance with increasing seasonality and decreasing rainfall (DeWalt *et al.* 2010; Schnitzer 2015), but has so far received little robust physiological explanations (Santiago *et al.* 2015).

Measures for π_{tlp} were consistent with the few direct observations of species vulnerability in long-term through-fall exclusion experiments in Amazonia (Chapter 2). The variability in π_{tlp} among species indicates the potential for a range of species responses to drought within Amazonian forest communities. This was further confirmed by direct monitoring of whole-plant water use during a marked dry season (Chapter 5). π_{tlp} values explained a significant part of variability in sapflow sensitivity to decreasing soil water content along the dry season. Leaf turgor-driven stomatal control and turgor loss may result in leaves acting as "safety valve" to prevent from xylem widespread cavitation (Tyree & Zimmermann 2002; Pivovaroff, Sack & Santiago 2014), as suggested by the often less negative π_{tlp} than threshold of xylem hydraulic failure in a compiled dataset for tropical trees. π_{tlp} may thus help quantify and model plant diverse performance under both regular and exceptional droughted conditions.

In the following, some perspectives of this work in forest modelling and ecophysiology are identified and discussed.

II. Perspectives

1. Modelling vegetation response to drought

The first and foremost obvious perspective of the different chapters of this thesis is the integration of an explicit water cycle and response to drought in TROLL. Alternative choices can be discussed and made in that respect, leading to further questions and model improvements.

a. Detailed versus integrated representation.

In most global dynamic vegetation models, the hydraulic soil-plant-atmosphere continuum is not explicitly represented and vegetation response to water stress is modelled using a soil water stress factor. This soil water stress factor is often computed as

$$\frac{\theta - \theta_{wp}}{\theta_{fc} - \theta_{wp}}$$

where θ is the soil water content, θ_{wp} is the soil water content at wilting point, and θ_{fc} is the soil water content at field capacity (Foley *et al.* 1996; Krinner *et al.* 2005; Clark *et al.* 2011). It is then used as a multiplier of various properties of leaf gas exchange (Egea, Verhoef & Vidale 2011; typically photosynthetic capacities and/or stomatal conductance) to simulate a decrease in plant carbon uptake and transpiration under water stress. Other versions of water stress factors exist, notably using soil water potential as a more relevant variable for plant than water content (Powell 2015; De Kauwe *et al.* 2015). But these factors depend only on soil properties and are the same across plant functional types. They have been found to limit the ability of models to describe vegetation response to drought (Powell *et al.* 2013; Joetzjer *et al.* 2014).

Models that simulate the whole soil-to-atmosphere water pathway have been developed, initially with a much finer-grained vegetation representation than DGVMs, and hence a limited spatial and temporal scope of simulations (Williams *et al.* 1996; Sperry *et al.* 2002; Fisher *et al.* 2006; Duursma, Medlyn & others 2012). This kind of representation have been recently coupled to implement a fine description of plant water use in large scale individual-based model (ED2, Moorcroft *et al.* 2001; Powell 2015; Xu *et al.* 2016; TFS,

Fyllas *et al.* 2014; Christoffersen *et al.* 2016). Additional modules of plant hydraulic architecture have also been added within the PFT-scheme of a few DGVMs (Hickler *et al.* 2006; Naudts *et al.* 2015). Comparison of alternative models that include or not plant diversity in drought-tolerance and plant water transport revealed that both are needed to suitably represent the response of vegetation to drought (Powell 2015; De Kauwe *et al.* 2015; Pappas, Fatichi & Burlando 2016).

b. Belowground processes

The first and foremost development required in TROLL to explicitly model the water cycle is the inclusion of a belowground space and water balance, which is still under development (G. Abou Mansour, master thesis, Toulouse). This includes vegetation rainfall interception, water run-off at the soil surface, infiltration and leakage (Fig. 1, Granier *et al.* 1999; Rodriguez-Iturbe *et al.* 2001; Wagner *et al.* 2011). Vegetation evapo-transpiration could then be fully coupled and simulated.
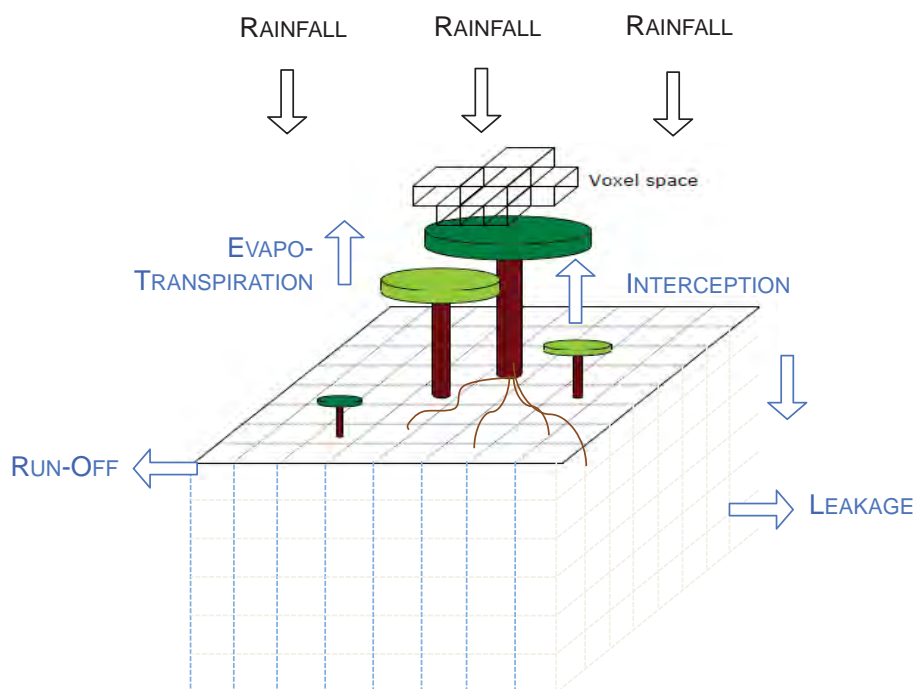

Fig. 1. Representation of individual trees in an explicit spatial grid in a forthcoming version TROLL that will include a belowground space and water balance (From G Abou Mansour).

Most of these processes are complex and non-linear, and alternative explicit computations exist, although a thorough review is not the scope of this discussion. Also, the

temporal and spatial scale to consider while modelling rainfall and subsequent water flow in the soil are multiple. The stochastic nature of rainfall events may question TROLL's current monthly timestep which may be reduced (Laio *et al.* 2001; Rodriguez-Iturbe *et al.* 2001)

As in the plant, water movement in the soil is driven by the different components of soil water potential (see Box 2 in general introduction). Similarly to cavitation that occurs in the xylem under water stress, cavitation can occur in the soil and breaks the soil-to-root water connection (Sperry *et al.* 2002; Fatichi, Pappas & Ivanov 2016). Belowground resistance may be a major cause of reducing water use during a drought event (Fisher *et al.* 2006). Soil conductance decrease, as well as the soil water content for a given water potential (Clapp & Hornberger 1978; van Genuchten 1980, Fig. 2), are highly dependent on its texture.
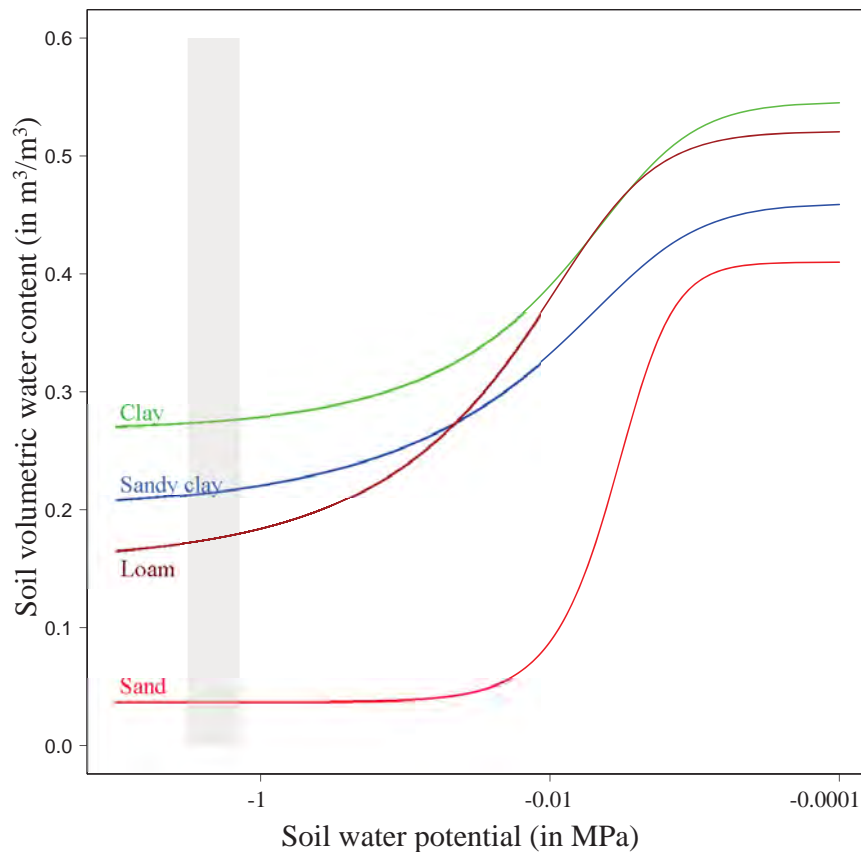
Fig. 2. Soil volumetric water content as a function of soil water potential, according to van Genuchten (1980) equation, for four different soil types. Parameters for clay, loam, sand and sandy clay soil are from Hodnett & Tomasella (2002). The grey vertical shaded zone corresponds to the range of leaf water potential at turgor loss point found in Chapter 2 of this thesis (Maréchaux *et al.* 2015).

In Figure 2 the soil volumetric water content is shown as a function of soil water potential for four different types of soils. From this figure, two main conclusions can be drawn. First, the different types of soil present contrasting water retention capacities and contrasting residual contents, as shown by their different maximum and minimum water content values. Plant

water stress has often been quantified as the cumulative difference of incoming rainfall and evapotranspiration, similarly across sites or region (e.g. maximum climate water deficit, Malhi *et al.* 2009; Chave 2014; Esquivel-Muelbert *et al.* 2016). However, this ignores that soil types are contrasted. Such a variation in soil properties limits our understanding of the spatial variation in the water deficit, and thereby its impact on the vegetation. Second, the range of plant critical water potential across species (e.g. leaf turgor loss point, grey zone in Fig. 2) corresponds to a relatively narrow range of soil water content whatever the soil. This may justify the use of a unique soil water content threshold per site beyond which the vegetation is critically vulnerable, despite various responses across species, as suggested by Meir *et al.* (2015b).

Overall, including the various effects of soil texture and water retention ability may allow TROLL to explore the variability of forest structure and function across site and various topography (Sabatier *et al.* 1997; Quesada *et al.* 2012). Explicitly modelling the soil water state dynamic may also be crucial to simulate soil respiration, as its dynamics may strongly contribute to terrestrial carbon sink variation (Townsend, Vitousek & Holland 1992; Meir, Cox & Grace 2006).

Explicitly accounting for root structure and function will be a second required development in order to simulate the whole plant water use, but also nutrient uptake (Bardgett, Mommer & De Vries 2014; Warren *et al.* 2015; Brunner *et al.* 2015). This development is facing two main challenges. First, roots have been critically understudied since they are much more difficult to measure than aboveground structure. Root traits have often been left off lists of important and commonly measured functional traits (see Table 1 in general introduction). If properties of coarse roots are likely related to wood traits (Fortunel, Fine & Baraloto 2012), coordination of fine root traits with other plant traits remain debated (Craine & Lee 2003; Tjoelker *et al.* 2005; Roumet *et al.* 2016). Also, very few studies have explored root depth directly in Amazonia (Humbel 1978; Nepstad *et al.* 1994; see also Jackson *et al.* 1996; Canadell *et al.* 1996). Deep roots may be an important feature to simulate transpiration maintenance during the dry season (Nepstad *et al.* 1994; Verbeeck *et al.* 2011). Second, fine roots are extremely dynamic, which challenges the approach of fixed species-specific traits (Warren *et al.* 2015). For example, neither tree size nor species might be a good predictor of root depth (Stahl *et al.* 2013) and root traits and biomass have shown important fluctuations with environmental conditions (Metcalfe *et al.* 2008; Lima, Miranda & Vasconcelos 2010; Bardgett *et al.* 2014).

    c.   Hydraulic trait coordination.

Whole-plant water transport involves a variety of structures and processes, whose modelling may require numerous parameters (e.g. Fig. 3). If data collection made during this PhD thesis represents a significant contribution to the available information on drought tolerance traits for Amazonian tree species, it focused mainly on one leaf-level trait. The leaf water potential at turgor loss point (π_{tlp}) has been found to reveal species distribution in regard to water supply (Bartlett *et al.* 2012b), community assemblage (Bartlett *et al.* 2015), or may inform whole-plant performance under drying conditions, as suggested in Chapter 5, however additional traits are needed to inform vulnerability to drought. For example the water potential at 50% loss of xylem conductance (P_{50}) has been found to be a better proxy of drought-induced tree mortality (Anderegg *et al.* 2016, Fig. 3).

       For tropical trees, data on xylem vulnerability to cavitation are sparse and mostly come from a few well-studied sites. Hence no data were available for Amazonian tree species in a recent compilation (Choat *et al.* 2012), and the few measurements that have been made since (e.g. Johnson *et al.* 2013; Rowland *et al.* 2015) produced 'r'-shaped curves whose reliability has been questioned (Choat *et al.* 2010; Cochard *et al.* 2010, 2013; but see Sperry *et al.* 2012; Jacobsen & Pratt 2012; Tobin *et al.* 2013; Hacke *et al.* 2015). Measurements of vulnerability to cavitation have been initiated as part of this work in French Guiana (WILT CEBA 2015 annual project). Considering the difficulties encountered to generate vulnerability curves on long-vessels species on the field, very few species were measured. This sampling should be extended in the future, but the current limit in data availability challenges our understanding of response to drought at the whole-plant scale.

       Coordination of hydraulic function at the whole plant scale have been repeatedly reported (Sack *et al.* 2003; Meinzer *et al.* 2008, 2009; Manzoni 2014; Klein 2014; Nolf *et al.* 2015; Pivovaroff *et al.* 2016; Chapter 5). However quantitative relationships are still mostly site-specific. Also bi-variate hydraulic trait trade-offs often appeared to be weak when expanded to large sets of species (Gleason *et al.* 2016; Chapter 5), illustrating the fact that plant hydraulic strategies do not lie on a clear one-dimensional functional axis or trade-off (Brodersen 2016; Pivovaroff *et al.* 2016). In recent modelling efforts, Xu *et al.* (2016) and Christoffersen *et al.* (2016), inferred π_{tlp} from leaf mass per area and wood density, and P_{50} from wood density. If this is a reasonable first step, the lack of strong mechanistic link between these drought-tolerance traits and these soft structural traits, as discussed in Chapter 2, calls for more direct inference (Fig. 3).

Also, species show diverse sensitivities in their stomatal and non-stomatal leaf photosynthetic processes under drought, which are both important to describe vegetation response in vegetation models (Manzoni *et al.* 2011; Zhou *et al.* 2013). Exploring the link between stomatal and non-stomatal limitation of photosynthesis and turgor-driven leaf impairment under on-going water stress will help model various changes in productivity and transpiration under water limitation (Fig. 3).

d. Allocation and stock

Incipient water stress first induces growth decrease, due to a reduction in cell turgor, expansion and division (Hsiao 1973; Muller *et al.* 2011; Fatichi *et al.* 2016). This may lead to an increase in allocation of photoassimilates to carbon reserve (non-structural carbohydrate, NSC; Sala, Woodruff & Meinzer 2012; Dietze *et al.* 2014), as observed on tropical trees during a dry season (Würth *et al.* 2005), and on taller trees, that are more prone to water stress, on Douglas-fir (Woodruff & Meinzer 2011). Productivity and growth are however mostly limited by photosynthesis in models, according to a carbon source-centred approach, such as in the TROLL model described in Chapter 1 (see Fig. 11 therein). Conversely, some model-data discrepancies call for an explicit representation of sink activities that themselves drive C assimilation and allocation (Le Roux *et al.* 2001; Fourcaud *et al.* 2008; Fatichi, Leuzinger & Körner 2014; Körner 2015). Water and nutrient limitation strongly influence the dynamic of sink activities, and should be explicitly integrated to move beyond the common carbon-centric approach (Körner 2015). The explicit integration of a NSC stock variable will be needed to well simulate these dynamics (Fig. 3).
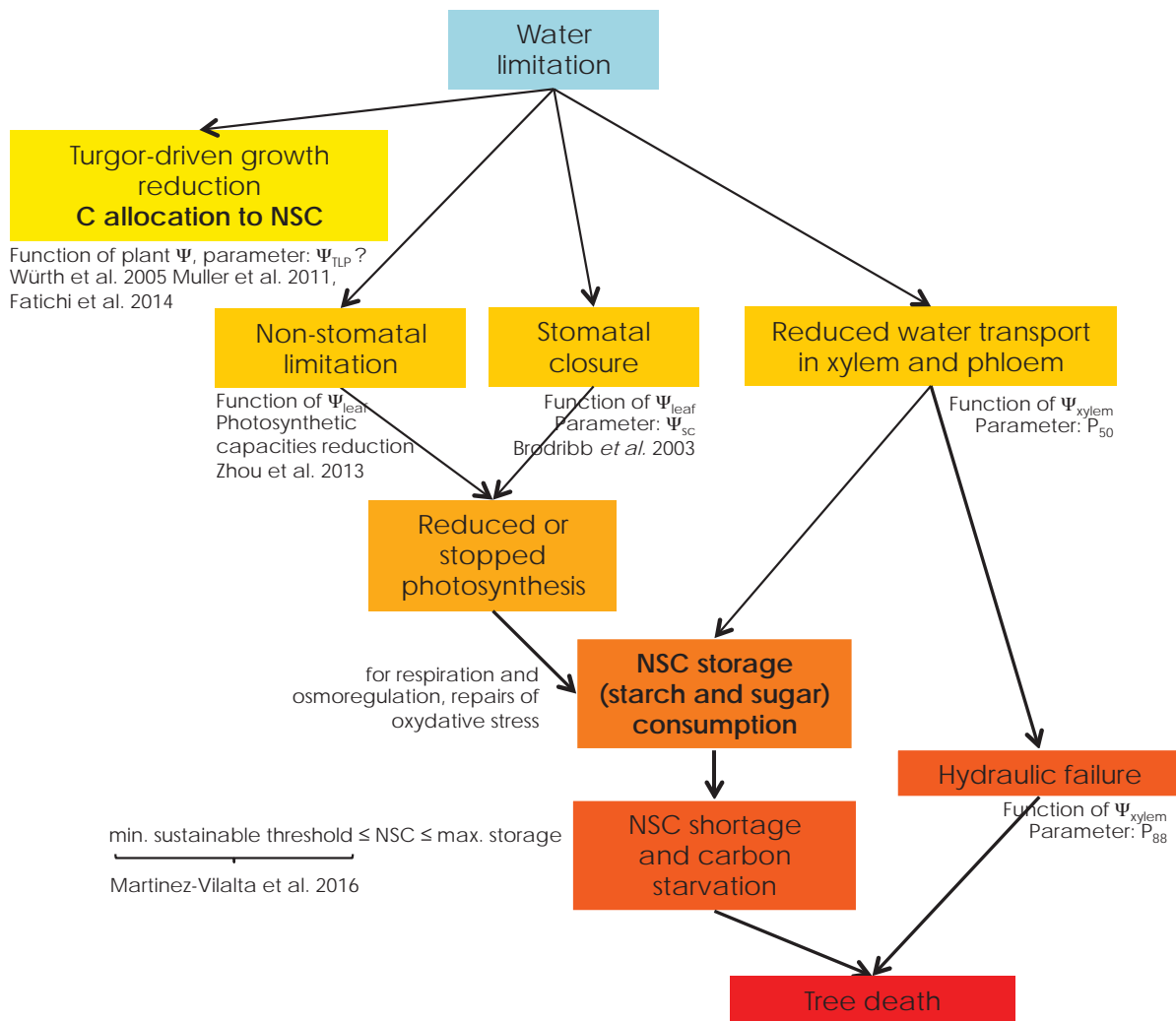
Fig. 3. Modelling tree responses to water limitation until death. Yellow to red colors correspond to the different effects from the first responses under incipient water stress until tree death (see also Fig. 14 in general introduction). Potential variables and parameters required to model these mechanisms are proposed. Each response may need a proper parameter; alternatively reported trait coordinations might be used (e.g. correlation between leaf water potential at stomatal closure, Ψ_{sc}, and leaf water potential at turgor loss point, Ψ_{tlp}, Brodribb *et al.* 2003; correlation between Ψ_{tlp} and xylem water potential at 50% loss of conductance, P_{50}, see chapter 5 and references therein). In bold is highlighted the role and use of a NSC individual variable.

The current understanding of storage processes has been limited by important methodological issues (Quentin *et al.* 2015) which impair model development (Dietze *et al.* 2014). A recent meta-analysis however showed that NSC account for ca. 10% of dry plant biomass and are highest in leaves (Martínez-Vilalta *et al.* 2016). It also highlighted a similar minimum NSC threshold among biomes and functional types (Fig. 3), as well as the importance to distinguish starch and sugar that have different functions and dynamics. Long-term NSC measurements, simultaneously to water potential and drought tolerance traits, may help model implementation of such dynamics. The development of remote sensing measurement of leaf non-structural carbohydrates concentrations at large scale by hyperspectral imagery may speed up such research program, if confirmed (Asner & Martin

2015). It would further shed light on the intensely debated relative rates and magnitudes of hydraulic failure and carbon starvation as triggers of drought-induced mortality (O'Brien *et al.* 2014; Hartmann 2015; Rowland *et al.* 2015; Fig. 3).

e. Modelling liana dynamics

Lianas are abundant in tropical forest (Schnitzer & Bongers 2002, 2011), and may even increase in abundance under changing climate and perturbations (Phillips *et al.* 2002; Laurance *et al.* 2013; Schnitzer 2015). Across the tropics lianas have been found to increase in abundance with decreasing rainfall and increasing seasonality (DeWalt *et al.* 2010). They may thus be particularly favoured under increasing drought intensity and frequency. As parasitic plants, lianas do not invest as much carbon as trees into stem construction, and represent a disproportionate amount of productivity and transpiration relative to their biomass (e.g. Restom & Nepstad 2001). Also, a liana-removal field experiment evidenced the substantial negative impact lianas have on tropical forest carbon storage (van der Heijden, Powers & Schnitzer 2015). Indeed lianas reduced by ca. 75% the forest carbon sink potential relative to control (removal experiment). These strong impacts on forest carbon cycle have called for an integration of lianas in new dynamic global vegetation models, as an additional plant functional type (Verbeeck & Kearsley 2016).

TROLL's code structure is well suited to account for lianas' impact on demographic processes. Its object-oriented code would allow the introduction of lianas as an additional class of object, whose individuals could independently affect individual trees by competing for the incident light on the tree crown and the belowground water and nutrient resources. If more experimental work and field measurements is crucially needed to well understand the liana growth syndrome (Schnitzer, Heijden & Powers 2016), and the liana clonal reproduction may challenge the individual-based representation (Ledo & Schnitzer 2014), models can be used to test alternative hypothesis on the mechanisms underlying lianas physiology and effects on trees.

2. Intra-specific variability and adaptive evolution

TROLL integrates a fine-grained description of taxonomic and functional diversity. However species traits are identical among the individuals of the same species. In its current version, TROLL thus assumes that species represent evolutionary stable traits associations and overlooks intra-specific functional variability. However, intra-specific variation may contribute to a substantial part of overall functional trait diversity and may be important for a range of ecological processes (Albert *et al.* 2010; Laughlin *et al.* 2012; Niinemets 2015; Le Bec *et al.* 2015).

We found limited variation among canopy tree π_{tlp} within an Amazonian forest site (Chapters 2, 3), yet drought-tolerance may however shift through ontogeny (Chapter 3), which may impact community composition (Poorter 2007; Fortunel *et al.* 2016). Vulnerability to cavitation may present a substantial intra-specific variability (Anderegg 2015; López *et al.* 2016) and has been found to increase with tree size (Rowland *et al.* 2015), which may be important in simulating the observed greater vulnerability to drought of taller trees (Bennett *et al.* 2015). Respiration and photosynthetic traits have shown strong within-canopy variation (Domingues *et al.* 2005; Ometto *et al.* 2006; Weerasinghe *et al.* 2014), which did not result from differences in stature across species alone. Accounting for trait variation with canopy depth improves model performance (Naudts *et al.* 2015; Coble *et al.* 2016). Also, significant trait variation between populations across environmental gradients can result from phenotypic plasticity (Laurans *et al.* 2012) as well as genetic adaptation, even at local spatial scale (Brousseau *et al.* 2013; Blackman *et al.* 2016). These processes may contribute to buffering the effect of climate change through new phenotypes better adapted to new conditions, particularly at species range borders (Parmesan 2006; Nicotra *et al.* 2010; Kramer *et al.* 2010).

The integration of evolutionary biology and ecosystem science has been emphasized as a crucial challenge in ecological modelling (Levin 1992; Matthews *et al.* 2011; Norberg *et al.* 2012; Scheiter, Langan & Higgins 2013; Grimm & Berger 2016; Urban *et al.* 2016). As an individual-based model that keeps track of species identity, TROLL includes the basic units of evolution, which acts on individuals through selection across generations. Evolutionary dynamics could be integrated in TROLL, through the addition of variance to the species-specific traits. This variability could then be inherited and result in an evolutionary adaptation thanks to the integration of an explicit seed class of object and the variation in recruit fitness

resulting from trait variation. Variation in seed dispersal ability across species should be better represented, by taking advantage of their reported dispersal mode (Hammond *et al.* 1996; Baraloto & Forget 2007), and pollen dispersal may also have to be considered (Aguilée *et al.* 2013). Also trait transmission from parents to seed and juveniles, should correspond to trait heritability, whose empirical determination requires a substantial amount of work (e.g. Franks, Sim & Weis 2007; Stanton-Geddes *et al.* 2013).

A related, although not equivalent, question concerns trait phylogenetic conservatism (Cornwell *et al.* 2014). If traits are conserved among closely related lineages, this may induce a directional loss of phylogenetic biodiversity under climate-induced range shifts (e.g. Comte, Murienne & Grenouillet 2014). For example, past drought in Amazonia may have shaped species evolution and current distribution of Neotropical trees (Mayle & Power 2008; Chave 2014), in synergy with other environmental filters (e.g. fire, soil texture, Quesada *et al.* 2012). In the Western Neotropics, the current distribution of tree species has been found nested along precipitation gradients, with most taxa being restricted to wettest areas, while drought-tolerant taxa being widespread (Esquivel-Muelbert *et al.* 2016). Phylogenetic conservatism of drought-tolerance traits (e.g. π_{tlp}, P_{50}, Maherali, Pockman & Jackson 2004) and hydraulic structures (stomata and vessel size and density, Boyce *et al.* 2009; Brodribb, Feild & Sack 2010) would critically help inform the future of biodiversity distribution under a drier climate.

3. Up-scaling individual-based models

The current generation of dynamic global vegetation models (DGVMs) strives to represent physiological and demographic processes while keeping computing time reasonable and spanning the globe. Individual-based models have proven useful in better representing these fine-scale processes, but their finer-grained representation have long been restricted to the stand scale, due to computational and data limitations. Several approaches have been proposed to up-scale individual-based models. Sato, Itoh & Kohyama (2007) simulated numerous representative vegetation stands distributed across space using a gap model, Moorcroft *et al.* (2001) developed a system of size- and age-structured partial differential equations to track the dynamic sub-grid-scale biotic heterogeneity, while Strigul *et al.* (2008) derived an approximation of individual-based model assuming perfect plasticity of crown shape, hence optimal allocation of leaves inside the canopy (the perfect plasticity

approximation). These approaches have paved the way to the integration of demographic processes in large-scale vegetation simulations. Shugart *et al.* (2015) recently proposed that the current development of computer and remote-sensing infrastructure allows considering individual-based models to simulate vegetation at large scales.

Using TROLL to simulate tropical forests at a regional scale is a challenging but stimulating goal. It would indeed open up its applications to other theoretical and practical questions such as the driver of floristic composition or the large scale impacts of land-use. The simulation of a 500-year long and 16-ha forest regeneration with a monthly timestep and a 1-m spatial resolution took ca. 90 min on a laptop (Chapter 1). If this is probably too large to reasonably consider extending the simulation to, for example, the whole of French Guiana (ca. 8,400,000 ha), coding a parallel version (as in Chave 1999) would result in substantial computer time reduction.
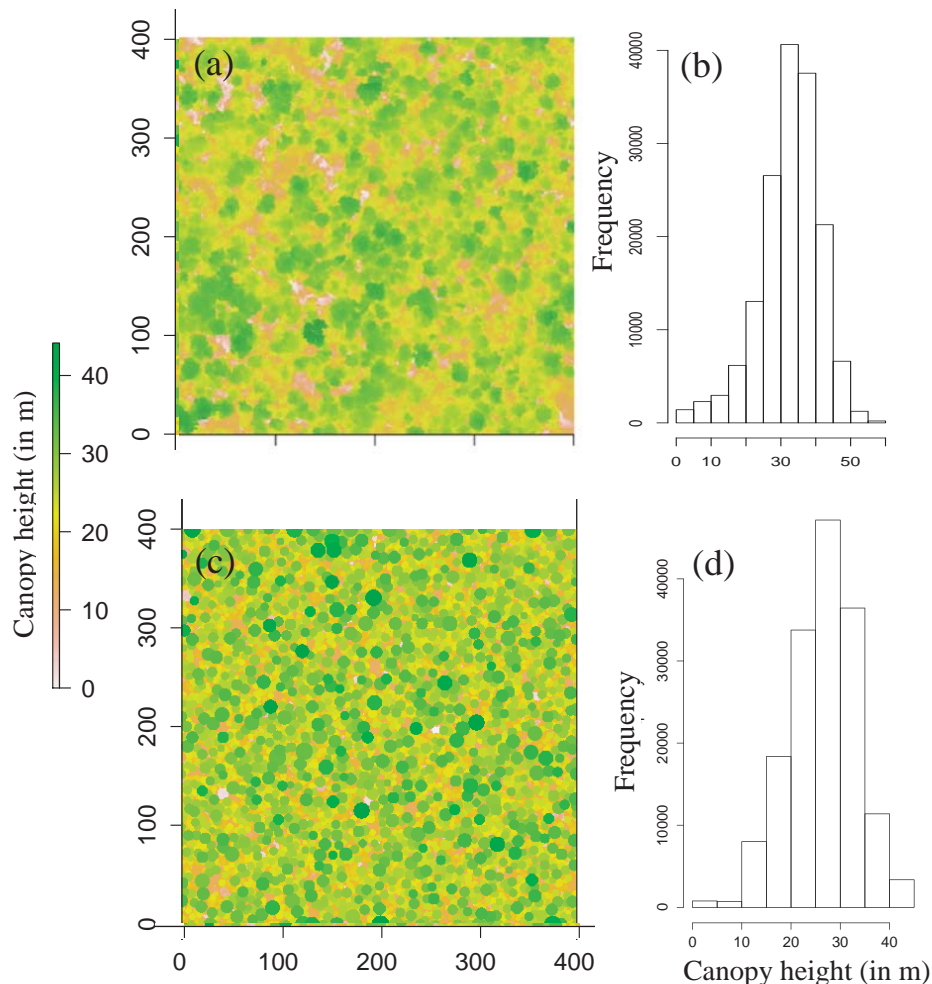
Fig. 4. Comparison of canopy height estimated from LiDAR acquisition and simulated by TROLL. (a) Map and (b) histogram of canopy height of a 400*400m square of the Nouragues Research Station area as inferred from a LiDAR-based model at 1-m resolution (Réjou-Méchain *et al.* 2015). (c) and (d) correspond to the map and histogram of canopy height of the 400*400m mature forest plot simulated by TROLL in Chapter 1. Frequency in histograms (b) and (d) refers to the number of 1m×1m pixels.

Networks of permanent forest plots and remotely sensed data would provide the information required to parameterize and validate such large-scale simulations (e.g. Fig. 4). LiDAR acquisition can inform on temporal and spatial forest structural changes, such as forest height and biomass (Réjou-Méchain *et al.* 2015). Radar technique can provide landscape and landform mapping at large scale (Guitet *et al.* 2013). Hyperspectral instruments, which sense light with many sensors, each covering a small wavelength width, has been shown to allow quantify chemical diversity (Asner *et al.* 2011). By fusing spectrometer data with coregistered LiDAR data on plant canopy structure, recent remote-sensing acquisition were able to provide crown-scale estimates for several leaf traits, including leaf nitrogen content, leaf phosphorous content, leaf mass per area or non-structural carbohydrate concentrations (Asner & Martin 2015; Asner *et al.* 2016). This makes it theoretically possible to assess functional and taxonomic diversity at large spatial scales (Asner & Martin 2009; Jetz *et al.* 2016) but also may facilitate the identification of species with a particular spectral signature (Féret & Asner 2011, 2014). The resolution of this large remotely sensed information matches the one of individual-based models' outputs (Fig. 4, Shugart *et al.* 2015). This information may also contribute to model improvement. For example, the seasonality in leaf fall and leaf area index is poorly understood in tropical rainforest (Wright & Cornejo 1990; Chave *et al.* 2010; Wu *et al.* 2016), hence poorly represented in models spanning different scales (De Weirdt *et al.* 2012; Xu *et al.* 2016), including TROLL (Chapter 1), but is however critical to explain tropical forest variation in productivity (Wu *et al.* 2016). LiDAR and hyperspectral data could inform the seasonality in LAI and its drivers.

III. On uncertainty in a changing world

Several developments in vegetation modelling are motivated by a reduction of uncertainties and data-model discrepancies. As a result, over the past years, models have steadily increased in complexity (e.g. ORCHIDEE, Krinner *et al.* 2005; Bellassen *et al.* 2010; De Weirdt *et al.* 2012; Naudts *et al.* 2015; FORMIND, Köhler & Huth 1998; Fischer *et al.* 2016). Despite this, models will always misrepresent some physiological processes or make assumptions away from biological realism, and absolute validation of a model of natural systems actually does not exist (Oreskes, Shraderfrechette & Belitz 1994). In that sense, modelling is the art of ignoring some processes. How much knowledge is needed on a biological process before it can be modelled? What are the relative virtues of complex versus more parsimonious models? These questions have long been debated in ecological science (Levins 1966; Evans *et al.* 2013b; a; Prentice *et al.* 2015), and to a large extent, there is not a single answer: knowledge arises from novel tools, not only from novel ideas (Dyson 2012).

Diverse inference approaches and methodological developments have been proposed to tackle the issue of constraining parameters uncertainties, which are further amplified by the desire to include additional processes (Wolf *et al.* 2011; Hartig *et al.* 2012; Lagarrigues *et al.* 2015; Courbaud *et al.* 2015; Urban *et al.* 2016). However, beyond predictions, models represent efficient tools to test hypothesis and guide the empirical development of knowledge (Rykiel Jr. 1996; Van Nes & Scheffer 2005; Norby *et al.* 2016; Medlyn *et al.* 2016).

There is an increasing demand for quantitative assessments in territories controlled by political and economic actors, and at local scales where most decisions, actions and impacts take place (Ostrom 2009). This often highlights the uncertainty associated with scientific models. For instance we may not be able to ascertain the precise temporal dynamics of species S that is being harvested, and it is difficult to know which local area will be the most impacted. However, in spite of quantitative limitations, qualitative predictions can be made with a high level of confidence. For example, we *do* know that tropical forests are vulnerable to drought events, especially if these are prolonged or repeated, inducing a decrease in carbon storage and change in composition. Likewise, we *do* know that the increasing anthropogenic emission of greenhouse gases induces a global warming and extreme climatic events, and that forest resistance and resilience to such changes is affected by fragmentation and degradation. Knowledge is increasing at an unprecedented pace. Networks of eddy-flux tower (Baldocchi

2003, 2008), remote-sensing products (Myneni *et al.* 2002; Le Toan *et al.* 2011; Jetz *et al.* 2016), distributed forest inventories (Malhi *et al.* 2002; Anderson-Teixeira *et al.* 2015) and experimental set-ups (Meir *et al.* 2015b; Norby *et al.* 2016), altogether screen tropical forest functioning, structure and composition at a range of scales and resolutions. Knowledge improvement is often concomitant with the raising awareness of system complexity. This leads to the paradoxical feeling that, as technical investigation is gaining ground, what we ignore is increasingly more important than what we know (Hansson 2002; Callon, Lascoumes & Barthe 2009).

Finally, uncertainties associated with the projected changes in anthropogenic pressures align with biophysical model uncertainties, or even overtake them. Alternative scenarios of greenhouse gases emissions (Nakicenovic *et al.* 2000) and land-use change (Schmitz *et al.* 2014) taken together, are a crucially important driver of the predicted fate of tropical forests (Betts *et al.* 2015; Lewis & Maslin 2015; Zhang *et al.* 2015). These alternative scenarios induce a large range in predicted states, which is actually not an *uncertainty*, but represents our societal leeway. It describes the possible effect of current and future decisions. Quantitative uncertainties may not prevent from informed actions to halting current threat of forest state and biodiversity (Urban 2015; Lewis, Edwards & Galbraith 2015). Adaptive management (Runge, Converse & Lyons 2011), best use of available data (Maréchaux, Rodrigues & Charpentier *in press*; Grantham *et al.* 2009), market incentive (Agrawal, Nepstad & Chhatre 2011), together with efficient networks of protected areas (Soares-Filho *et al.* 2006; Ricketts *et al.* 2010; Nolte *et al.* 2013) can all contribute to reaching a goal of "development without destruction" (Lewis *et al.* 2015). Halting deforestation (United Nations 2014), developing sustainable agricultural exploitation (Raison *et al.* 2015), implementing low-impact logging methods of timber production (Merry *et al.* 2009; Bicknell *et al.* 2014) are the tools of our policy leeway (Lewis *et al.* 2015). These should be implemented in a network of diverse governance systems, operating across scales (Ostrom *et al.* 1999). "Acting in a uncertain world" (Callon *et al.* 2009) is both possible and necessary. Both modelling exercise and experimental approaches feed knowledge and enlighten choices regarding such a complex and diverse ecosystem that represent tropical forests.

"While waiting for the certainties resulting from [scientific] projections to become available – especially in view of the irreversibility of some of the processes unleashed - prudence is the better part of valor and is in any case an imperative of responsibility."

Hans Jonas
The Imperative of Responsibility: In Search of an Ethics for the Technological Age.
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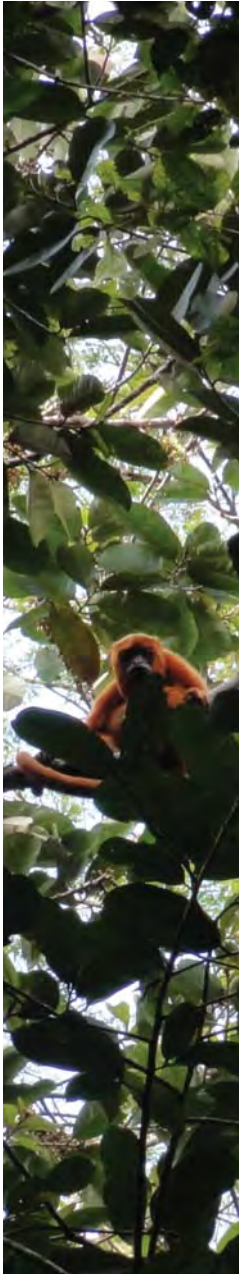
APPENDIX

TROLL code structure

General information

TROLL forest simulator is encoded in C++. Two specific classes of object are defined and used: a *Tree* class and a *Species* class. Each *Tree* object points to a *Species* object. There are as many *Tree* objects as there are sites (or pixels). For clarity's sake while reading the code, each member variable of the *Tree* and *Species* classes begins by t_- and s_- respectively.

General parameters of the simulation, species-specific parameters and climate data are provided in a unique input file, whose structure must be thoroughly kept while modifying parameter values.

The simulation itself is made by the *Main* function, which calls to separate functions or methods (i.e.. member functions of the *Tree* and *Species* classes), so that the code is modular and the different processes are modeled and can be modified independently. Alternative options may be included for particular processes, and a TROLL user may want to activate some options or not by defining or not some *macros* at the very beginning of the code (*define/undef*, preprocessor directives).

The *Main* function has three arguments, set by the user. The first argument corresponds to the absolute pathway and name (with extension) of the input file, preceded by "-i", the second argument corresponds to the absolute pathway and name the code should use to create the output files of the simulation, preceded by "-o", and a third argument corresponds to the number of the simulation, preceded by "-n".

In the following description, the code functioning is described step by step, as it truly runs, and not as it is written. This may help well understand how it is built and debug any potential error. Only basic options of processes that may be alternatively modeled in a more complex way are here described.

Main program

– Assignment of the global variables *bufi* and *buf*, with the pathway and names passed in arguments for the input and output files respectively. A third argument is used to number the simulation, when several independent simulations are launched automatically simultaneously.

– Initialization of the random number generators, using both the current time and the simulation number, to ensure that different simulations launched at the same time or not will have different random chains.

– Opening of the following output files:

  *buf*_par in *out* stream
  *buf*_info in *out2* stream

↓

Initialise(); Initialization routine

  – Opening of the intput file:

    bufi in *In* stream

  – Assignment of the simulation parameters and of the variables common to all species from the input file stream *In*.

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– Conversion of all length variables in number of horizontal or vertical cells.
– Writing of the basic simulation features in the *buf_info* output file.
– Dynamic allocation of *T*: initialization of one *Tree* object per site (member variables set to zero by the *Tree* constructor).
– Dynamic allocation of *S*: initialization of (*numesp* + 1) *Species* objects.

↘

Species::Init(); Species initialization

– Allocation of the *Species* member variables, from the input file stream *In*, other member variables are computed from these input parameters.
– Conversion of length member variables in number of horizontal or vertical cells.
– Dynamic allocation of the species' *s_Seed*: initialization to 0 in all sites.

– Dynamic allocation and initialization of the climate variables.
– Writing of all the parameters from the input file stream *In* into the *buf_par* output file.
– Opening of the following output files:

buf_abund]in *sor*[0] stream
buf_abu10 in *sor*[1] stream
buf_abu30 in *sor*[2] stream
buf_ba in *sor*[3] stream
buf_npp in *sor*[4] stream
buf_ppfd0 in *sor*[5] stream
buf_state in *sor*[6] stream
buf_dbh in *sch*[1] stream
buf_vertd in *sch*[2] stream

↓

AllocMem(); Dynamic memory allocation

– Assignment of *HEIGHT*, *RMAX*, *SBORD* and *dbhmaxincm*.
– Dynamic allocation of *nbdbh*, *layer*, *tempch*, *tempch2* (used for the output files), of *ESP_N* (used for local germination in *UpdateTree*), of *LAI3D* (all voxel values initialized at 0).

↓

BirthInit(); Initial non-local germination

– Loop over *S*: for each species, loop over the *s_nbext* incoming seeds: for each incoming seed, one site is drawn at random; if no tree is already occurring at this site (*T*[*site*].*t_age*==0), birth of one tree of this species at this site.

↘

Tree::Birth(); Tree initialization

– Birth of one tree at the site in argument: initialization of the *Tree* member variables, with tree size variables (*t_dbh*, *t_Tree_Height*, *t_Crown_Radius* and *t_Crown_Depth*) set to the corresponding initial parameters (*DBH0*, *H0*, *ra0* and *de0*) provided in input and identical for all species; the initial leaf density (*t_dens*) is also prescribed (*dens*), and the leaf area only attributed to young leaves (so that, *t_youngLA=t_leafarea*, and *t_matureLA=t_oldLA=0*) and deduced from leaf density and crown dimensions; *t_PPFD*, *t_D* and *t_T* are computed by *Fluxh* called at *t_Tree_Height*.

$\searrow$

| Tree::Fluxh(); | Mean micro-climate at a given height within a tree canopy.

The climatic variables computed by *Fluxh* correspond to the mean per time step of daily maximal light flux, VPD and temperature.

- Computation of the average light flux received by the tree at height h according to Beer-Lambert law as

$$\frac{\sum_{\substack{\text{crown's voxels v} \\ \text{at height h}}} Wtot \times \exp(-LAI3D(v) \times klight)}{\text{number of crown's voxels at height h}}$$

here equal to *Wtot*, since *LAI3D* was initialized to 0.
- The mean vapor pressure deficit and temperature are also updated from *LAI3D* values at h and following empirical relationships.

- Computation of *t_GPP* in $gC.timestep^{-1}$, using *Species::dailyGPPleaf*(*t_PPFD*, *t_D*, *t_T*):

$\searrow$

| Species::dailyGPPleaf(); | Daily mean leaf-level assimilation rate

- Computation of daily mean assimilation rate, by calling *Species::GPPleaf* with half-hourly values (i.e. 48 values for 12 hours of daily light) of light flux, vapor pressure deficit and temperature. These half-hourly values are computed from the daily maximum values (*t_PPFD*, *t_D*, *t_T*) multiplied by the averaged normalized (between 0 and 1) daily variation of light flux, VPD and T, provided in input (*daily_light*, *daily_vpd*, *daily_T*).

$\searrow$

| Species::GPPleaf(); | Leaf-level assimilation rate

- Computation of the leaf-level assimilation rate, co-limited by incident light and CO_2 supply, according to the Farquhar-von Caemmerer-Berry model, in $micromolC.m^{-2}.s^{-1}$. Temperature-dependent values of photosynthetic parameters are computed from global or species-specific parameter values. The leaf internal C concentration, required in the FvCB model, is computed from VPD according to a model of stomatal conductance provided by Medlyn *et al.* (2011).

- Computation of temperature-dependent leaf and stem maintenance respiration (branch and root respiration are assumed equal to a fixed proportion of leaf and stem respiration), and computation of *t_NPP* as the net balance between gross primary production minus maintenance and growth respiration.
- Increment of the number of individuals of the tree's species (*nblivetrees* and *s_nbind*).

- Increment of the total number of individuals *nblivetrees* with each species' number of trees (*s_nbind*).

$\downarrow$

- Closing of the output stream *out*.
- Declaration and initialization to 0 of time variables (for the simulation's duration).
- Loop over the number of iteration (*iter*): set of the climate variables for the iteration and call to *Evolution*.

$\downarrow$

| Evolution(); | Forest evolution at each iteration

$\searrow$

| UpdateField(); | Update of the LAI and seed fields

– **LAI3D computing**:

- Reinitialization of *LAI3D* to 0 in all voxels.
- Loop over all sites: for each tree, addition of its contribution to *LAI3D*, using *Tree::CalcLAI*:

  ↘

  | Tree::CalcLAI(); | Tree's contribution to the LAI3D field

  – Loop over the tree crown's voxels: incrementation of *LAI3D* at each voxel by *t_dens*.

- *LAI3D* computing by summing voxels' LAI3D from the canopy top to the ground.

– **Evolution of the field *Seed***:

- **Seeds production by mature trees**: loop over the sites, if a tree occurs there ($t\_age > 0$), call to *Tree::DisperseSeed*

  ↘

  | Tree::DisperseSeed(); | Dispersion of the tree's seeds

  – if the tree is mature, receives enough light (more than $2 \times s\_LCP$), loop over the *nbs* produced seeds:
  - Each seed is dispersed at a distance ρ (random variable following a normal law of mean $d + Crown\_Radius$) with an angle θ (random variable following a uniform law on $[0; 2\pi]$).
  - *s_Seed* is updated at the site of dispersion:

    ↘

    | Species::FillSeed(); | Update of the species seeds field with the tree's seed

    – Creation of a new seed at the given site in the species' *s_Seed*.

- **External seed rain**: constant flux from the metacommunity.
  Loop over the species: for each species, loop over the *s_nbext* incoming seeds: for each incoming seed, one site is chosen randomly, *s_Seed* is set to 1 at this site.

↘

| UpdateTree(); | Germination, death, growth of trees and update of the species seed field.

– **Local germination**:
  Loop over the sites: if no tree occurs at this site yet, all species with a seed present at this site are listed in *ESP_N*, and then, one species is randomly chosen among them; if there is enough light (above *s_LCP* and computed with *LAI3D* according to Beer-Lambert law): birth of a tree of this species at this site:

  ↘

  | Tree::Birth(); | Tree initialization

  – Birth of one tree at the site in argument: initialization of the *Tree* member variables, with tree size variables (*t_dbh*, *t_Tree_Height*, *t_Crown_Radius* and *t_Crown_Depth*) set to the corresponding initial parameters (*DBH0*, *H0*, *ra0* and *de0*) provided in input and identical for all species; the initial leaf density (*t_dens*) is also prescribed (*dens*), and the leaf area only attributed to young leaves (so that, *t_youngLA=t_leafarea*, and *t_matureLA=t_oldLA=0*) and deduced from leaf density and crown dimensions; *t_PPFD*, *t_D* and *t_T* are computed by *Fluxh* called at *t_Tree_Height*.

$\searrow$

| Tree::Fluxh(); | Mean micro-climate at a given height within a tree canopy.

The climatic variables computed by *Fluxh* correspond to the mean per time step of daily maximal light flux, VPD and temperature.

- – Computation of the average light flux received by the tree at height h according to Beer-Lambert law as

$$\frac{\sum\limits_{\substack{\text{crown's voxels}\\\text{at height h}}} Wtot \times \exp(-LAI3D(v) \times klight)}{\text{number of crown's voxels at height h}}$$

- – The mean vapor pressure deficit and temperature are also updated from *LAI3D* values at h and following empirical relationships.

– Computation of t_GPP in $gC.timestep^{-1}$, using *Species::dailyGPPleaf* (t_PPFD, t_D, t_T):

$\searrow$

| Species::dailyGPPleaf(); | Daily mean leaf-level assimilation rate

- – Computation of daily mean assimilation rate, by calling *Species::GPPleaf* with half-hourly values (i.e.. 48 values for 12 hours of daily light) of light flux, vapor pressure deficit and temperature. These half-hourly values are computed from the daily maximum values (t_PPFD, t_D, t_T) multiplied by the averaged normalized (between 0 and 1) daily variation of light flux, VPD and T, provided in input (*daily_light*, *daily_vpd*, *daily_T*).

$\searrow$

| Species::GPPleaf(); | Leaf-level assimilation rate

- – Computation of the leaf-level assimilation rate, co-limited by incident light and CO_2 supply, according to the Farquhar-von Caemmerer-Berry model, in $micromolC.m^{-2}.s^{-1}$. Temperature-dependent values of photosynthetic parameters are computed from global or species-specific parameter values. The leaf internal C concentration, required in the FvCB model, is computed from VPD according to a model of stomatal conductance provided by Medlyn *et al.* (2011).

– Computation of temperature-dependant leaf and stem respiration (branch and root respiration are assumed equal to a fixed proportion of leaf and stem respiration).
– Increment of the number of individuals of the tree's species (*nblivetrees* and *s_nbind*).

– Variables of death counting (*nbm_n1* and *nbm_n10*) set to zero.
– **Tree evolution**:
Loop over the sites: trees are updated at each site.

$\searrow$

| Tree::Update(); | Tree death or growth

If $t\_age > 0$, either death or growth:

- – **Death**, occurs with a probability equal to the tree death rate computed by *Species::DeathRate*. If so the tree dies and depending of the trees' t_dbh, either *nbm_n1* or *nbm_n10* is incremented.

↘

Species::DeathRate(); Species' death rate

– Computation of the tree death rate, equal to a basal rate which depends on species tree density (a species with a denser wood having a lower death rate) and incremented if the light received by the tee is lower than the species light compensation point (s_LCP) and if the tree is in a state of prolonged negative carbon balance, both leading to carbon starvation.

↘

Tree::Death(); Tree death

– Tree's member variables are reinitialized.
– Decrement of the species' number of individual (s_nbind).

– **Growth** otherwise:

↘

Tree::Growth(); Tree growth

– **Tree carbon uptake**: computation of t_GPP, by summing GPP from each tree crown layer (loop over the tree crown depth from t_Tree_Height - t_Crown_Depth to t_Tree_Height), computed using *Species::dailyGPPleaf(t_PPFD, t_VPD, t_T)* with each layer environment drawn from *Tree::Fluxh*:

↘

Tree::Fluxh(); Mean micro-climate at a given height within a tree canopy.
The climatic variables computed by *Fluxh* correspond to the mean per time step of daily maximal light flux, VPD and temperature.

– Computation of the average light flux received by the tree at height h according to Beer-Lambert law as

$$\frac{\sum\limits_{\substack{\text{crown's voxels v} \\ \text{at height h}}} Wtot \times \exp(-LAI3D(v) \times klight)}{\text{number of crown's voxels at height h}}$$

– The mean vapor pressure deficit and temperature are also updated from *LAI3D* values at h and following empirical relationships.

↘

Species::dailyGPPleaf(); Daily mean leaf-level assimilation rate

– Computation of daily mean assimilation rate, by calling *Species::GPPleaf* with half-hourly values (i.e.. 48 values for 12 hours of daily light) of light flux, vapor pressure deficit and temperature. These half-hourly values are computed from the daily maximum values (t_PPFD, t_D, t_T) multiplied by the averaged normalized (between 0 and 1) daily variation of light flux, VPD and T, provided in input (*daily_light*, *daily_vpd*, *daily_T*).

↘

Species::GPPleaf(); Leaf-level assimilation rate

– Computation of the leaf-level assimilation rate, co-limited by incident light and CO_2 supply, according to the Farquhar-von Caemmerer-Berry model, in $micromolC.m^{-2}.s^{-1}$. Temperature-dependent values of photosynthetic parameters are computed from global or species-specific parameter values. The leaf internal C concentration, required in the FvCB model, is computed from VPD according to a model of stomatal conductance provided by Medlyn *et al.* (2011).

– **Tree carbon balance**: computation of temperature-dependent leaf and stem maintenance respiration (branch and root respiration are assumed equal to a fixed proportion of leaf and stem respiration), and computation of *t_NPP* as the net balance between gross primary production minus maintenance and growth respiration.

– **Allocation of biomass to wood growth and size increment**: update of *t_dbh* from the gain of volume resulting from the new biomass allocated to wood (*t_NPP* multiplied by a currently fixed factor *fallocwood*) and assuming isometric growth of the stem; updates of *t_Crown_Radius*, *t_Crown_Depth* and *t_Tree_Height* from the updated *t_dbh* and allometric equations.

– **Allocation of biomass to leaf production and leaf demography**: biomass allocated to leaves leads to production of young leaves (*flush*, expressed in leaf area using *s_LMA*), leaf age pools (in leaf area) are updated, with a fraction (determined using *s_time_young*) of young leaves becoming mature, a fraction (determined using *s_time_mature*) of mature leaves becoming old, and a fraction (determined using *s_time_old*) of old leaves falling and producing litter (*t_litter*, expressed in mass, using *s_LMA* to match with measurements usually reported from litter traps).

– **Update of tree leaf density**, *t_dens*, from the updated tree leaf total area (*t_leafarea*) and crown volume.

– Increment of *t_age*.

– **Update of the seed field**: loop over the sites: for each site, loop over the species: for each species, update of *s_Seed* at this site with *Species::UpdateSeed*

↘

| Species::UpdateSeed(); | Seed's age increment depending of the dormancy duration

– If the site is occupied by a tree (*T[site].t_age > 0*), *s_Seed* set to 0 at this site.
– Otherwise, if *s_Seed* at this site equal to the specie seed dormancy duration (*s_dormDuration*), then *s_Seed* set to 0 at this site, else increment of *s_Seed* at this site.

↘

| Average(); | Computation of simulated plot average features every timstep

– Loop over the species: for each species, *s_chsor[i]* set to 0 for each i.
– Writing of the current timestep *iter* in each output stream *sor[i]*.
– Loop over the species: for each species, the average number of individuals per hectare is written in *sor[0]*.
– *nblivetrees* set to 0.
– Loop over the sites: for each site, if a tree occurs at this site, increment of *nblivetrees* and data are added to the tree's species's *s_chsor* with *Tree::Average*:

↘

| Tree::Average(); | Individual tree's contribution to plot features

– If the tree's age is strictly positive:

- Increment of *s_chsor[1]* if the tree's dbh is bigger than 0,1.
- Increment of *s_chsor[2]* if the tree's dbh is bigger than 0,3.
- Increment of *s_chsor[3]* with t_dbh^2 (for basal area).
- Increment of *s_chsor[4]* with $t\_NPP \times 10^{-6}$.
- Increment of *s_chsor[5]* with $t\_GPP \times 10^{-6}$.
- Increment of *s_chsor[7]* with tree aboveground biomass (according to Chave *et al.* 2014 relationships).
- Increment of *s_chsor[8]* with $t\_Rday \times 10^{-6}$ (daily leaf maintenance respiration).
- Increment of *s_chsor[9]* with $t\_Rnight \times 10^{-6}$ (nighttime leaf maintenance respiration).
- Increment of *s_chsor[10]* with $t\_Rstem \times 10^{-6}$ (stem maintenance respiration).
- Increment of *s_chsor[9]* with $t\_litter \times 10^{-6}$ (leaf litter fall).

– Loop over the species: for each species *s_chsor* values are divided by the number of hectares.
– Writing sum across species in *sor* output streams:

- Total number of live trees in *sor[0]*.
- Total number of live trees with a dbh > 0,1 in *sor[1]*.
- Total number of live trees with a dbh > 0,3 in *sor[2]*.
- Total basal area in *sor[3]*.
- Total net primary production in *sor[4]*.
- Total gross primary production in *sor[5]*.
- Total basal area with only tree with a dbh ¿0.1 in *sor[6]*.
- Total aboveground biomass in *sor[16]*.
- Total leaf daytime maintenance respiration in *sor[143]*.
- Total leaf nighttime maintenance respiration in *sor[144]*.
- Total stem maintenance respiration in *sor[145]*.
- Total leaf litterfall in *sor[150]*.

– Computation of the mean light flux reaching the soil, with a loop over the sites, and writing of it in *sor[7]*.
– Writing of number of tree deaths in *sor[8]*.

↘

OutputField(); Simulation results output

– With the frequency determined by *frequout*:

- Loop over the sites: computation of *nbdbh* with *Tree::histdbh();*.

↘

Tree::histdbh(); Tree's contribution to the dbh histogram

– Increment of *nbdbh* at the tree's dbh (in cm).

- Loop over the height and sites: computation of the average LAI per height (*layer*).
- Output of the dbh histogram (*nbdbh*) in *sch[1]*.
- Output of the average LAI per height in *sch[2]*.

– End of the evolution loop (*nbiter* calls to *Evolution();*).
– Writing of the effective CPU simulation time in the *buf_info* file.

↓

Free::Mem(); Free dynamic memory

– **THE END**.

Isabelle MARECHAUX

Individual-based modelling of tropical forests: role of biodiversity and responses to drought.

Supervisor: Jérôme CHAVE

Abstract:
A great part of uncertainties in our current understanding and projections of the carbon cycle lies in the vegetation compartment. The problem of biodiversity representation in vegetation models has long been an impediment to a detailed understanding of ecosystem processes. The high biodiversity of tropical forests, their disproportionate role in global biogeochemical cycles, together with their vulnerability to direct and indirect anthropogenic perturbations, amplify the relevance of this research challenge. In particular, the predicted increase in drought intensity and frequency in the tropics may impact forest structure and composition, as already observed in natural and artificial experiments. This thesis explores how new advances in modelling and ecophysiology should help improve our understanding of these processes in the future.

In the first chapter, I describe an individual-based and spatially-explicit forest growth simulator, TROLL, that integrates recent advances in plant physiology. Processes are linked to species-specific functional traits parameterized for an Amazonian tropical rainforest. This model is used to simulate a forest regeneration, which is validated against observations in French Guiana. Model sensitivity is assessed for a number of key global parameters. Finally, we test the influence of varying the species richness and composition on ecosystem properties.

Tropical forest response to drought is not well understood, and this hampers attempts to model these processes. In chapters 2 to 5 I aimed at documenting drought-tolerance and its diversity in an Amazonian forest. A rapid method of determination of a leaf drought tolerance trait, the leaf water potential at turgor loss point (π_{tlp}), was validated and applied to a range of plant species. We established the first community-wide assessment of drought tolerance in an Amazonian forest. These results inform on the drivers and determinants of leaf drought tolerance, across tree species and lianas, tree size, successional stages, light exposition, and seasons. Variability in π_{tlp} among species indicates the potential for a range of species responses to drought within Amazonian forest communities. This is further confirmed by direct monitoring of whole-plant water use on diverse canopy trees during a marked dry season.

Finally, I discuss the implications of these results to increase the dialogue between the vegetation modeling community and ecology, to enhance model's predictive ability, and to inform policy choices.

Key-words: biodiversity, tropical forests, individual-based modelling, functional trait, drought, tolerance, turgor loss point, Amazonia, French Guiana.

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Résumé :
La faible représentation de la biodiversité dans les modèles de végétation a longtemps été un obstacle à la compréhension et à la projection des processus écosystémiques. La forte biodiversité des forêts tropicales, leur rôle clé dans les cycles biogéochimiques globaux, ainsi que leur vulnérabilité aux perturbations anthropiques directes et indirectes, amplifient les difficultés et enjeux de ces questions de recherche. En particulier, l'augmentation prédite de la fréquence et de l'intensité des sécheresses pourrait impacter la structure et composition floristique de ces forêts, comme dors et déjà observé au cours d'expériences naturelles et artificielles. Cette thèse explore ces questions de recherche à travers deux approches complémentaires, de modélisation et de mesures écophysiologiques.

Dans le premier chapitre, je décris un simulateur de croissance forestière individu-centré et spatialement-explicite, TROLL, qui intègre les progrès récents en physiologie des plantes. Les processus sont paramétrés à l'aide de traits fonctionnels espèce-spécifiques, pour une forêt tropicale amazonienne. Une régénération forestière est simulée, et validée par des observations faites en Guyane française. La sensibilité du modèle à plusieurs paramètres globaux clés est évaluée. Enfin, l'influence de la variation de la richesse et composition spécifiques sur les propriétés écosystémiques est explorée.

La réponse des forêts tropicales à la sécheresse est mal connue, empêchant la représentation pertinente des processus en jeu dans les modèles de végétation. Les chapitres 2 à 5 de cette thèse ont ainsi pour but de documenter la tolérance à la sécheresse et sa diversité dans une forêt amazonienne. Une méthode récente et rapide de détermination d'un trait de tolérance des feuilles à la sécheresse, le potentiel hydrique des feuilles au point de perte de turgescence (π_{tlp}), est validée et utilisée, permettant de quantifier pour la première fois un tel trait de tolérance à la sécheresse dans une forêt amazonienne à l'échelle de la communauté. Ce jeu de données permet l'exploration des déterminants de la tolérance à la sécheresse des feuilles, à travers les espèces d'arbres, les tailles des individus, les stades de succession, les expositions à la lumière, ainsi que les lianes. La variabilité de π_{tlp} observée suggère une large diversité de réponses à la sécheresse au sein des communautés de plantes amazoniennes. Ceci est confirmé par le suivi direct du flux de sève au cours d'une saison sèche sur divers arbres de canopée.

Enfin, je discute les implications de ces résultats pour le développement des futurs modèles de végétation.
Mots-clés : biodiversité, forêts tropicales, modèle individu-centré, trait fonctionnel, sécheresse, tolérance, point de perte de turgescence, Amazonie, Guyane française.