Chapter Six

Floristic shifts versus critical transitions in Amazonian forest systems

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6.1 Introduction

Tropical forests hold close to 250 Pg of carbon, with Latin America contributing half of this (Saatchi et al. 2011). Although the rates of deforestation appear to have decreased over the past decade, tropical deforestation still represents the bulk of the c. 1.1 PgC yr$^{-1}$ of C emissions due to land-use change (Friedlingstein et al. 2010). The direct impact of deforestation and degradation has the potential to be mitigated through a performance-based mechanism such as REDD (Reducing Emissions from Deforestation and Forest Degradation), by monetising carbon held in both managed and unmanaged forests (Agrawal, Nepstad & Chhatre 2011). Additionally, tropical forests contribute to a terrestrial carbon sink (Le Quéré et al. 2009), offsetting fossil carbon emissions into the atmosphere through a physiological response of the vegetation (Lewis et al. 2009; Lloyd & Farquhar 2008). Thus tropical forests offer critically important ecosystem services by reducing the short-term effect of anthropogenic carbon emissions into the atmosphere.

However, in the face of global climate trends, the resilience of tropical forests has been called into question (Cox et al. 2000). South America is sensitive to a number of large-scale climatic anomalies, including the El Niño Southern Oscillation, the Pacific Decadal Oscillation and the North Atlantic Oscillation. All of these contribute to displacing the yearly course of the Inter-Tropical Convergence Zone (ITCZ) and increase the strength of the dry season in some regions (Garreaud et al. 2009; Marengo 2004). The 2005 and the 2010 climatic events over Amazonia have exemplified these atmospheric regime shifts, and these may occur more frequently during the twenty-first century. As a result of the increased likelihood of severe droughts, models suggest that Amazonian forests may shift by 2100 to a different biome type akin to a woodland savanna or dry forest (Cox et al. 2000, 2004; Huntingford et al. 2008; Malhi et al. 2009; Poulter et al. 2010). Aside from the radical implications for human and wildlife populations inhabiting Amazonia, this new biome type would have far less potential to hold carbon, and such a shift...
would have important consequences for global life support services. Some of the predictions of this ‘Amazon dieback’ scenario have been empirically tested (Phillips et al. 2009). Theoretical work has also attempted to understand whether a shift showing alternative stable states is a likely outcome. Within a realistic range of precipitation regimes, a stability analysis comparing the current cover of three biome types – forest, savanna and treeless areas – has shown that forest and savanna do appear to behave as alternative stable states, substantiating the claim that climate change may trigger a critical transition from forest to savanna (Hirota et al. 2011; Staver, Archibald & Levin 2011). Although this approach needs to be backed by more empirical studies and confirmed by more detailed simulations, it appears to be a universal feature of tropical biome dynamics (Murphy & Bowman 2012). Thus, this body of knowledge collectively suggests that Amazonian forests are functioning today at the verge of a major environmental tipping point.

Support for the Amazon dieback scenario is one of the major findings of a new generation of Earth models where atmospheric global circulation models (GCMs) are synchronously coupled to dynamic global vegetation models (DGVMs). These DGVMs have a long tradition in vegetation modelling (Cramer et al. 2004; Krinner et al. 2005; Sitch et al. 2003), being related to the development of agricultural or forestry management models (Shugart 1984) and to the need to model short-term fluxes between atmosphere and biosphere in atmospheric physics. Here, I discuss two limitations of existing DGVMs that have until now been seldom addressed, but that are especially critical for an accurate modelling of tropical old-growth forests and woody savannas alike.

First, few DGVMs attempt to account for demographic stochasticity, in spite of the importance of these local processes in explaining the dynamics of unmanaged vegetation (Purves & Pacala 2008). One notable exception is the Ecosystem Demography model (ED model; Fisher et al. 2010; Moorcroft, Hurtt & Pacala 2001), where demographic stochasticity was taken into account through a spatial averaging procedure inspired from statistical physics (Iwasa, Andreasen & Levin 1987). With increased computer power, an alternative to the ED modelling strategy is to develop individual-based DGVMs for forests, for example Sato, Itoh and Kohyama’s (2007) ‘SEIB-DGVM’. While important efforts have been made in this direction in the recent literature, fusing ecosystem science and community ecology certainly represents a central challenge in the construction of a new generation of Earth models (Fisher et al. 2010).

A second limitation is that biodiversity is only simplistically represented in the current generation of DGVMs. Usually, a pool of only 10 or so plant functional types (PFTs) are available for populating DGVMs (Sitch et al. 2003), just two of which occur in tropical forests: tropical broadleaf evergreen trees
(woody vegetation with persistent leaves), and tropical broadleaf raingreen
trees (semi-deciduous woody vegetation). Within a grid cell of c. $1^\circ \times 1^\circ$ latitude/longitude, a fraction of each PFT is competing for space and resources. This simplification is easily understandable in view of the complexity of the task of modelling the interaction between a plant canopy and the atmospheric boundary layer (Jones 1992). However, what is known of the adaptive potential of organisms in changing environments (Davis, Shaw & Etterson 2005; Duputié et al. 2012) and of the evolutionary history of tropical tree families (Jaramillo et al. 2010; Wing et al. 2009) demands a critical reappraisal of over-simplistic approaches.

In this chapter, I examine lines of evidence for or against the Amazonian dieback scenario in light of ecological theory and palaeoenvironmental evidence. I then argue that a new generation of DGVMs must appropriately account for the physiology of tropical trees, including the contribution of both photosynthetic organs and the rest of the plants. I separate the contribution of photosynthetic organs (leaves) and of the rest of the plants (especially the stem and branches). Finally, I describe a possible implementation of this approach in an individual-based forest growth simulator.

6.2 The stability of Amazonian forests: historical insights

Tropical rain forests have been a dominant vegetation type on the Earth for much of the past 100 Ma. In his wonderful book on the evolution of tropical rain forests, Morley (2000) provided a synthesis of the fossil evidence for the tropical forest flora. Solid evidence now exists for the presence of multi-storeyed angiosperm-dominated forests from the late Cretaceous (Morley 2011), or in the early Tertiary for the Neotropics (Burnham & Johnson 2004; Wing et al. 2009). This suggests that the rise to dominance of tropical rain forests preceded the Cretaceous–Tertiary transition. This claim was also supported by molecular dating of phylogenetic trees for two predominantly tropical forest clades, the Malpighiales (Davis, Shaw & Etterson 2005), and the Ericales (Sytsma et al. 2006). A continuous palynological record dating back to 65 Ma BP from Colombia has confirmed that at least some areas in northern South America have been dominated by tropical forest taxa for much of the period from the Early Paleocene to the Early Miocene (Jaramillo, Rueda & Mora 2006), although a lot of vegetational changes have taken place over this period (Jaramillo, Rueda & Mora 2006; see also Jaramillo et al. 2010; Rull 1999). Together with the evolution of C4 photosynthesis, the rise to dominance of tropical rain forests is probably one of the very few key evolutionary advances in the history of terrestrial vegetation over the past 100 Ma (Brodribb & Feild 2010; Christin et al. 2008; McAdam & Brodribb 2012; Morley 2011).

Focusing on the Quaternary, oxygen isotope data from Brazil speleothems spanning the past 200 ka demonstrate that the climate of South America has
been altered by fluctuations in solar radiation, coupled with a large reorganisation of equatorial atmospheric circulation that led to a change in the position of the ITCZ (Cruz et al. 2009; Wang et al. 2007). Carbon isotope evidence from the Cariaco Basin, Venezuela, over the past 50 ka, suggests that the South American climate has been subject to large-scale oceanic shifts in the Atlantic meridional overturning circulation (Hughen et al. 2004). These climatic changes have been also traced in water level changes over the past 160 ka for Lake Pata, Brazil, close to the equator (Bush, Silman & Urrego 2002). Other areas of Amazonia appear to have been floristically quite stable over the past 50 ka, where the pollen cores show a dominance of arboreal pollen taxa, and little grass pollen, through much of this period (Burbridge, Mayle & Killeen 2004; Bush, Silman & Urrego 2004; Colinvaux, de Oliveira & Bush 1996; Haberle & Maslin 1999), except in an area that is today close to the forest–savanna ecotone: Serra dos Carajás, Brazil (Aby et al. 1991).

By far the most controversial climate-induced paleoecological event in South America is the one that occurred during the last glacial maximum (LGM), around 21 ka BP. There is evidence for a decline in precipitation and a decrease in temperature by up to 5 °C in some parts of this continent (Bush, Silman & Urrego 2004), in an atmosphere with CO2 levels about half of those recorded today. Some authors have used this evidence to suggest that Amazonian forests were largely converted into savannas during the glacial periods. This fragmentation of Amazonian forests has been put forward as an explanation for the high diversity of this biome: many populations may have been maintained in allopatry through long periods in the Quaternary during which repeated episodes of forest fragmentation acted as a ‘pump of speciation’ (Bush 1994). Yet, there is no evidence for a widespread transition from a closed-canopy forest to a woodland savanna system either in the paleoecological record (Bush, Silman & Urrego 2004; Colinvaux et al. 2000; Haberle & Maslin 1999; Mayle et al. 2004, 2009) or in modelling studies (Cowling, Maslin & Sykes 2001). The pollen records reported by Colinvaux, de Oliveira and Bush (2000) and by Burbridge, Mayle and Killeen (2004) suggest that glacial-age Amazonian forests, with their mix of currently Andean and lowland Amazonian taxa, have no modern analogues. Pennington et al. (2000) proposed that in the LGM much of the current extent of the Amazonian forest was occupied by the now geographically restricted seasonally dry tropical forests. Together these studies suggest that a precipitation level of as much as 25% lower than today, and both lowered temperature and CO2 concentration, did not result in a radical shift to an alternative stable state during the LGM. Rather, there was a smooth transition involving changes in the floristic assemblage, while maintaining a continuous canopy cover.

The LGM has often been perceived as the hallmark of past climatic changes. However, Amazonian paleoecology teaches us that tropical forests may have
undergone the most radical transition much later, during the Holocene. Over 30 years ago, Servant et al. (1981) were the first to provide evidence for arid phases in Bolivia during the Holocene; much more evidence has accumulated recently. For instance, there is evidence of an important dry event at around 7–5 ka BP (Absy et al. 1991; Burbridge, Mayle & Killeen 2004; Mayle et al. 2004), and this has recently been confirmed with a larger array of techniques (Bird et al. 2011; van Breukelen et al. 2008). This period of increased drought occurrence may have played a prominent role in the history of human populations in this region, as suggested by evidence from crop domestication (Piperno 2011). Figure 6.1 shows one of the few palynological cores in French Guiana (Ledru 2001). The peak in the pollen of pioneer species (Cecropia and Vismia), lasting over two centuries between around 1500 and 1300 BP, was attributed to either a human disturbance or to a sustained climatic event (grey peak close to the C14 calibration point at 1570±50 BP, see also Bird et al. 2011 for a comparable drought around 1500 BP in Peru). The Holocene history of northeast Amazonia remains poorly documented, but recently Freycon et al. (2010) used soil carbon isotope composition to detect whether past vegetation may have been dominated by plants with a C4 photosynthetic pathway.

![Figure 6.1](https://example.com/figure6.1.png)

**Figure 6.1** A 3000-yr palynological record, from a peat bog at the Nouragues Ecological Research Station, French Guiana. Redrawn from Ledru (2001).
(essentially savanna grasses), which show a lower $^{13}\text{C}$ discrimination than arboreal taxa (predominantly of the C3 photosynthetic pathway). They showed that even forest sites close to coastal savannas today have remained forested during much of the Holocene. Together, this suggests that even though Amazonian forests have been through important climatic fluctuations during the Holocene, they have been quite resilient to these changes.

How does the history of tropical forests help shed light on their future? It is likely that the future environmental conditions of tropical America will be very different from that of the LGM. Precipitation will not necessarily be less than today, but the frequency of long droughts is likely to increase, a phenomenon that may have occurred episodically from 10 to 6 ka BP (Mayle et al. 2009). In addition, atmospheric CO$_2$ concentrations and temperature will increase (Salazar, Nobre & Oyama 2007), and deforestation will contribute to altering the regional climate (Poulter et al. 2010). Comparing LGM simulations with those of vegetation status under projected climates by the end of the twenty-first century, Cowling, Cox and Betts (2004) showed that the likely feedbacks responsible for maintaining the integrity of Amazonian forest cover in the past were a reduction in both evapotranspiration (related with reduced rainfall) and plant respiration (related with lower temperature). This combination of response leading to a lower net primary productivity (NPP) but also a lower metabolism is unlikely to hold in the future. For these reasons, Cowling, Cox and Betts (2004) suggested that the Amazonian forest is near its resilience threshold.

This analysis calls for a more in-depth study of the resilience concept. Resilience is the capacity of an ecosystem to absorb disturbance without shifting to an alternative state and losing ecological functions (Holling 1973). Thus resilience encompasses two processes: ‘resistance’, the ability of a system to withstand a disturbance, and ‘recovery’, the ability of the system to return to its initial, pre-disturbance, state. This distinction largely depends on how frequent the disturbances are: if the shocks occur frequently and stochastically, the impact of these shocks depend on the ecosystem’s resistance. If the perturbations occur rarely, ecosystem stability will be measured by the rate at which the system returns to equilibrium (Ives & Carpenter 2007). The LGM scenario of a shift in floristic composition within a persistent tropical forest canopy cover is consistent with the view of a ‘resistant’ system. Forests have been able to reshuffle their floristic makeup so as to maintain fundamental ecological functions (water recycling, carbon storage, radiation balance). It also appears that tropical forests have an ability to recover from pronounced disturbances, even though this recovery may take centuries (Ledru 2001; Mayle et al. 2009). This prediction is consistent with the idea of biodiversity conferring ‘insurance value’ (Yachi & Loreau 1998). Some tree species are dominant today because they are adapted to current local
environmental conditions. However, the large reservoir of species spanning a wide range of ecological functions enables the tropical forest system to navigate through a variety of pulse perturbations. Currently dominant species may decline in abundance under changing environmental conditions, but be replaced by other species that are rare today.

The consequence of this discussion is that the current classification of vegetation into a few PFTs ignores an important potential for the adaptation of ecological species assemblages to future climates. Current DGVMs therefore misrepresent the community-wide potential of the vegetation to adapt ecologically to novel environmental conditions. Next, I explore evidence in favour of this claim.

6.3 The leaf economics spectrum and the physiology of tropical trees

A great amount of work has been devoted to identifying PFTs within plants generally, and tropical tree species specifically, with the aim of simplifying the apparently overwhelming biological diversity of these ecosystems (Favrichon 1994; Picard & Franc 2003; Swaine & Whitmore 1988). The underlying theory of PFTs is that species in a given environment may be simply ranked along an axis of performance and persist in coexistence thanks to an ecological trade-off (Grime 1979; Swaine & Whitmore 1988). This idea is reminiscent of Robert MacArthur’s model (1972) of a trade-off between ecological strategies with fast-growing species that die young (the r strategists) versus slow-growing species that survive for a long time (the K strategists). If this theory is valid, then functional traits should all covary along a single axis, and it is thought that carbon assimilation traits should thus suffice to describe the plant ecological strategy spectrum. This includes, in addition to competitive and successional traits, ecological traits that describe cold or drought tolerance (Harrison et al. 2010); drought tolerance is discussed further below.

Much of the physiological machinery implemented in current versions of DGVMs is based on a leaf-level view of plant physiology. Leaves are the most important organs for carbon fixation, and a general model of photosynthesis has been developed for them (Leuning et al. 1995; von Caemmerer 2000). Non-woody plants dominate a sizeable fraction of the planet’s vegetation, and by focusing on leaf traits alone a universal way to classify plants into functional types becomes possible (Wright et al. 2004). As a result, an active field of research has been concerned with classifying plant species into PFTs using measurable leaf-level traits, or leaf functional traits (Cornelissen et al. 2003; Wright et al. 2004). These traits include such measures as total leaf area, leaf width, specific leaf area (leaf area per unit dry mass), elemental concentration in leaves (C, N, P and major elements like K, Ca, Mg, Al, Fe), and discrimination of stable isotopes of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$). In addition, leaf
mechanical properties have been included in these multi-factorial analyses, and the implications for defence have been discussed (Onoda et al. 2011; Read & Stokes 2006). These traits are easily collected across a large number of plants and facilitate the compilation of global datasets (Kattge et al. 2011).

Numerous reports of the cross-species variation of some of these traits have been published across biomes (Wright et al. 2004), or within tropical rain forests (Baraloto et al. 2009; Fyllas et al. 2009; Ometto et al. 2006). They point to a cross-biome universality of leaf traits. Wright et al. (2004) showed that, across biomes, species mean traits fell into a single universal surface in a foliar functional trait space, confirming the idea that some trade-off explains the covariation of functional strategies, thus defining the leaf economics spectrum. Recently Fyllas et al. (2009) have carried out an extensive study of regional-scale variation for a range of foliar functional traits in Amazonian tree species to test the pertinence of a leaf economics spectrum within tropical vegetation biomes. They conclude that variation in key foliar functional traits is associated with variation in tree growth. For instance, high fertility soils are associated with higher growth rates, lower leaf mass per area (LMA, the inverse of specific leaf area) and higher nutrient concentration per dry weight (N, P, K and Mg). Trees growing on more fertile soils have more nutrients (especially N and P) to invest into the photosynthetic apparatus, hence the correlation observed by Fyllas et al. (2009). This result provides strong, albeit correlative, support for developing DGVMs parameterised with foliar functional traits (Clark et al. 2011; Mercado et al. 2011). It is consistent with the broadly accepted assumption that PFTs can be defined by a simple suite of foliar traits.

The above PFT classification assumes that carbon assimilation is the major limiting factor in plant growth. However, short but stressful events may considerably compromise the fitness of populations, leading to an increased death rate and/or to reduced overall performance. The likelihood of sudden events that considerably reduce the population fitness has been explored in much greater detail for plants growing in the temperate zone where frost tolerance is an important dimension of the phenological timing of trees (Chuine 2000). In the tropics, one of the most important of these stressful events is the occurrence of prolonged drought periods (McDowell 2011). At an ecosystem scale, it has been demonstrated experimentally that droughts have a significant short-term impact on the ecosystem functioning of tropical forests (Markewitz et al. 2010). At the plant scale, stomatal closure is the main line of defence against drought, but beyond a certain point cell turgor will be lost, leading to leaf wilting (Nobel 2009). The ability of an ecosystem to withstand severe droughts depends on the ability of the species to resist wilting. It has thus become a major quest to find functional plant traits that would correlate with drought tolerance.
Recently, Bartlett, Scoffoni and Sack (2012) have provided a useful perspective on the issue of measuring leaf tolerance to drought. They have demonstrated that, across biomes, leaf water potential at wilting (or at turgor loss point, $\Pi_{\text{tlp}}$) is the best predictor of leaf drought tolerance. Leaf water potential at turgor loss point is a negative pressure (measured in MPa) since water is in tension within the leaf. Drought is measured by the soil negative pressure imposed upon the water column of the plant. If soil water potential falls below a threshold (often assumed to be $-1.5$ MPa), ecosystem-wide consequences for plant survival are to be expected. Several responses are possible in dry conditions. The plant may reduce its tolerance through osmotic regulation, leading to a reduction in $\Pi_{\text{tlp}}$ (Nobel 2009). This plasticity is limited, however (Wenhui & Prado 1998; Zhu & Cao 2009). Deciduous plants drop their leaves before they wilt, to save as much water as possible. Importantly, deciduousness in dry tropical forest species is not only aimed at maximising water use efficiency, but appears to be primarily a herbivore avoidance, or phenological escape, strategy (Janzen 1981; Marquis, Morais & Diniz 2002). Prado et al. (2004), in a detailed study of a range of cerrado plant species, have shown that during the dry season, evergreen species such as *Didymopanax vinosum* Cham. & Schlecht maintain their photosynthetic capacity ($A$) at the same time as regulating evapotranspiration ($E$) to levels comparable to that of the wet season. In contrast, deciduous species (e.g.* Bauhinia rufa* (Bongard) Stendel) regulate their water use efficiency ($A/E$) by reducing both $A$ and $E$. The leaf turgor loss point is also often lower in evergreen species than the average community, although the relationship between deciduousness and tolerance to leaf wilting is not clear (Wenhui & Prado 1998).

Figure 6.2 represents the covariation of leaf water potential at the turgor loss point against the ratio of wet to dry mass of leaves. It summarises a number of interesting findings. First, the dry forest species of Hao et al. (2008) tend to have a lower $\Pi_{\text{tlp}}$ than the moist forest species of Zhu and Cao (2009), as also pointed out by Bartlett et al. (2012). There appears to be a relatively good correlation between $\Pi_{\text{tlp}}$ and the ratio of wet to dry mass of leaves ($r^2 = 0.63$). Second, a phylogenetically controlled comparison between dry forest species and woodland savanna species (the grey circles and grey triangles, respectively, in Figure 6.2) suggests that $\Pi_{\text{tlp}}$ is not necessarily lower in woodland savanna species than in adjacent dry forest species. Pending more detailed studies, this suggests that the phylogenetic signal is low for $\Pi_{\text{tlp}}$. Further genus-specific leaf tolerance studies, in *Cordia* (Choat, Sack & Holbrook 2007) and *Ficus* (Patiño et al. 1995), deserve to be mentioned in this respect. Third, Zhu and Cao’s (2009) study confirms that osmotic regulation, leading to a drop of $\Pi_{\text{tlp}}$ between the wet and the dry season, is an important component of drought tolerance. Remarkably, the three liana species studied by Zhu and Cao (2009) show little to no osmotic regulation. Fourth, and
finally, lianas’ leaf water potential at the turgor loss point does not differ from that of trees, in spite of their propensity to keep their leaves even in semi-deciduous forests (Schnitzer & Bongers 2002).

Do some commonly measured leaf traits covary strongly with leaf tolerance to wilting? Niinemets (2001) has proposed that LMA should be a good correlate of drought tolerance because it is associated with leaf wall stiffness. However, Bartlett, Scoffoni and Sack (2012) showed that LMA is a poor predictor of $\Pi_{tlp}$ measurements globally, suggesting that leaf wall stiffness as an indicator of leaf drought tolerance does not hold globally across plants. In the few publications focusing on dry tropical environments, a relatively good correlation has been found between leaf drought tolerance and LMA (Bucci et al. 2004; Meinzer et al. 2008a; Poorter et al. 2009), but this evidence remains too thin to discount the possibility that $\Pi_{tlp}$ may represent an independent axis of variation in the leaf economy spectrum, and that drought tolerance is inadequately

Figure 6.2 Correlation between the leaf turgor loss potential ($\Pi_{tlp}$, in MPa) and the ratio of wet mass over dry mass for leaves. Grey symbols are from Hao et al. (2008), black symbols are from Zhu and Cao (2009). In Hao et al.’s (2008) study, six congeneric species pairs were compared, where each pair has one forest species (grey circles) and one cerrado species (grey triangles). In Zhu and Cao’s (2009) study, six species were measured both in the wet season (black circles) and in the dry season (black triangles). Species denoted with (L) in Zhu and Cao’s (2009) study are lianas.
represented in the analysis by Wright et al. (2004). Besides, LMA is associated with other functions as well, and it is also a remarkably plastic trait (Poorter et al. 2009).

6.4 Whole-plant physiology of tropical trees

A second important issue relevant to the construction of PFTs is that tropical trees are not just leaf surfaces. Most of their carbon is held in self-supporting structures (trunks) and resource-foraging structures (roots). Leaf water is supplied through the xylem, and the whole plant water status is critically dependent on the health of woody tissue. Wood protection in particular may represent a non-negligible energetic investment for a tropical tree, as suggested by the variation in bark thickness across tree species (Brando et al. 2012; Paine et al. 2010). Much research has been conducted on wood structure, because tropical timber represents an important international economic market. Wood production is a critical allocation strategy for photosynthates, since growth in height leads to a competitive advantage in forested environments. Many wood functional traits may be measured that are likely to be even more important in predicting tree growth rates than leaf-level traits. For instance, just by looking at a wood core in the trunk of a tropical tree, critical demographic data may be inferred quite easily, at least if the tree shows an annual growth pattern (Rozendaal & Zuidema 2011; Worbes 2002).

Simple functional traits have been proposed for inclusion in DGVM development, such as wood density, or the distribution of conduit sizes (Chave et al. 2009; Patiño et al. 2009; Zanne et al. 2010). Wood density has generated a great deal of recent interest because it is believed to integrate a number of important stem processes (Baas et al. 2004). It has been speculated that wood density may correlate with the ability of a woody plant to withstand whole-plant water stress (Hacke et al. 2001; Jacobsen et al. 2005; see also below). Wood density is also clearly related to tree mechanical stability (Chave et al. 2009; van Gelder, Poorter & Sterck 2006), and correlates negatively with mortality rates across a broad range of forests (Kraft et al. 2010). Finally, wood density has been found to be strongly related to total stem sapflow, and thus total plant transpiration, in a limited number of studies (Bucci et al. 2004, 2008; McCulloh et al. 2011; Meinzer et al. 2008a).

In addition to causing leaf wilting, drought may cause irreversible damage to the plant as a result of cavitation in the xylem conduits (Cochard 2006; Tyree & Zimmermann 2002). Xylem failure during exceptional episodes of drought may occur more frequently in the future. Engelbrecht and Kursar (2003) have demonstrated that seedlings of a range of species respond very differently to drought stresses. Seedling drought tolerance may indeed be a critical element of the fitness of tree populations in seasonal climates, and a key explanation of patterns of plant distribution across environmental
gradients (Engelbrecht et al. 2007). However, rapid changes in climate may also increase the risk of xylem failure of large trees. For instance, Zhang et al. (2009) have shown that larger individuals of the legume tree *Sclerolobium paniculatum* were more likely to show branch damage and to die than smaller trees under the same drought conditions (see Rood et al. 2000 for a temperate tree example). This shows that DGVMs should pay special attention to modelling xylem-failure induced mortality in trees, and not only mortality related to carbon starvation (see e.g. Fisher et al. 2010; McDowell 2011). An obvious trait to model the risk of xylem failure is the pressure at which a stem has lost 50% of its hydraulic conductivity ($P_{50}$). In their meta-analysis, Maherali et al. (2004) reported 41 $P_{50}$ measurements for moist tropical forest species (mostly from Tyree, Patiño & Becker 1998 and Zotz, Tyree & Cochard 1994), and only 19 for dry tropical forest species. They found that vulnerability to cavitation was on average almost three times larger in moist tropical forest than in dry tropical forest trees. Additional values not included in Maherali et al.’s (2004) compilation for dry and moist tropical forests confirm this first analysis (Brodribb et al. 2003; Bucci et al. 2006; Chen et al. 2009; Lopez et al. 2005; Markesteijn et al. 2011; Meinzer et al. 2003, 2008b; Zhu & Cao 2009; see Figure 6.3, and appendix). Figure 6.3 shows that moist tropical forest species appear to be more vulnerable to drought-induced xylem failure than dry forest or woodland savanna species. However, with the exception of Meinzer et al. (2003, 2008b), these previous studies have tended to ignore

![Figure 6.3 Xylem vulnerability to cavitation (pressure at which 50% of the xylem hydraulic conductivity has been lost) for dry and moist tropical forests. This meta-analysis shows that dry forest species are on average half as vulnerable to xylem cavitation as moist tropical forest species. The mean values are drawn as grey horizontal lines (mean $P_{50} = -2.66$ MPa, $n = 33$, for dry tropical forests; mean $P_{50} = -1.41$ MPa, $n = 66$, for moist tropical forests). However, the range of variation is large and comparable in both biome types.](image)
the species that dominate Amazonian forests. Thus this conclusion merits further scrutiny in this region. Xylem water potential at 50% loss of hydraulic conductivity varies a lot across species in both biomes, and spans almost the same range of variation. This is suggestive that, under a stronger drought, more species may be at risk in moist tropical forests than in dry tropical forests, yet the survivors may be enough to maintain a closed-canopy cover and a large fraction of the biomass stocks.

How should we account for non-leaf traits in the development of DGVMs? Under MacArthur’s (1972) trade-off theory, whole-plant traits should covary in a predictable way and define simple plant ecological ‘syndromes’. For instance, fast-growing trees should also invest less into wood construction costs because they invest more into photosynthesis (per dry mass). Although such a trade-off in allocation is expected across broad environmental gradients and across biomes, this pattern does not appear to hold within moist tropical forests. Baraloto et al. (2010) showed that leaf traits are not correlated with stem-related functional traits, and the leaf-investment and stem-investment strategies appeared to be uncorrelated. Thus, for PFTs based on leaf traits, it is impossible to predict how the plant will allocate carbon into wood production. Further, based on this analysis it is expected that species able to invest a lot in both wood and leaf construction can still persist in the ecosystem. Chen et al. (2009) arrived at a similar result, using more traits but only six species in the family Euphorbiaceae s.l. Fyllas, Quesada and Lloyd (2012) have taken this idea one step further through a global approach based on functional traits measured not only on leaves but also on whole plant traits, including wood traits. They conducted an ordination analysis on a suite of traits, much like Baraloto et al. (2010) but at a regional scale, and subsequently clustered the species into discrete groups using a K-mean cluster algorithm. They found that their species could be naturally clustered into four groups, possibly defining novel types of PFTs. These four groups correspond to a combination of light demand strategies (as measured by potential gas exchange rates) and overall tree stature. However, there was still large variation in species traits within each of these four PFTs. It should be noted that the uncoupling of leaf and stem traits remains a debated subject. Leaf and wood traits appear to be more correlated in xeric habitats than in moist forest ones. Indeed, the two studies where a convergence of wood and leaf traits was observed were conducted in woodland savanna and dry forest (Bucci et al. 2004; Mendez-Alonzo in press).

The special case of lianas merits a separate discussion. Tropical forests are remarkable for having a large abundance of lianas (Schnitzer & Bongers 2002), which may increase in abundance with changing climates (Phillips et al. 2002). These lianas, as parasitic plants, do not need to invest as much carbon into wood construction. They have large conduits and a higher water conductivity
leading to higher transpiration (Andrade et al. 2005; Feild & Balun 2008; Zhu & Cao 2009). Lianas thus represent a disproportionate amount of carbon turnover (NPP) and of ecosystem transpiration in comparison with the biomass they hold (e.g. Restom & Nepstad 2001). They also have a distinctive response to drought, since many lianas of semideciduous forests keep their leaves during the dry season (Schnitzer & Bongers 2002; see also Figure 6.2). It would be important to further appraise the importance of accounting for the presence of lianas in DGVMs and to model their contribution to NPP and to ecosystem transpiration. Likewise, other life forms found almost exclusively in moist tropical forests, such as hemiepiphytes, may play an important ecosystem-level role (Patiño et al. 1995; Zotz, Tyree & Cochard 1994).

In conclusion, in spite of an enormous effort to better understand the physiology of tropical plants, a number of key points remain undocumented, especially regarding the drought tolerance of large tropical trees. As a result, current efforts to reduce these physiological behaviours to a few discrete groups have not met with great success. Most attempts to construct plant functional types have been restricted to leaf traits (Schulze et al. 1994; Wright et al. 2004), and available evidence now suggests that existing trait databases do not include appropriate proxies for xylem conductivity and for xylem vulnerability to cavitation. Comparing a range of species with respect to different ecological functions, it has often been found that traits sometimes covary but cannot easily be partitioned into discrete groups (Baraloto et al. 2010; Goldstein et al. 2008; Figure 6.3). This argument should not be overlooked when considering plant functional types as an operational concept in the building of dynamic vegetation models. It is possible that PFTs could be replaced with more detailed population-based models that couple the dynamics of the species assemblage with ecosystem processes, or that many more PFTs could be included to account for the observed variability in plant traits.

6.5 Discussion
The idea that the presence of a few species may help the persistence of ecological functions through environmental disturbances is far from novel in ecology and has been widely discussed in the ecosystem science literature. However, evidence for such a scenario is wanting in tropical forests because it is difficult to reconcile the long generation times of tree species, and the hypothetical nature of environmental change scenarios, with any experimental test. Here, I have shown that the current generation of coupled biosphere–atmosphere Earth models still include too many uncertainties when it comes to making predictions about the future of Amazonian tropical forests. If the Amazon dieback scenario has spurred considerable controversy, evidence in its favour remains scarce, and existing models produce very different projections for Amazonia at the end of the twenty-first century. However, global
trends of an increase in temperature will probably be accompanied by stronger and/or more frequent droughts over Amazonia. Research on drought tolerance of Amazonian forests remains surprisingly scarce given the importance of the challenge, but available evidence suggests that both the leaves and the xylem of average moist tropical forest tree species are not as well adapted to drought as dry tropical forest and woodland savanna species. Thus, whether drought-tolerant trees will be able to supplant drought-intolerant ones within the moist tropical forest matrix, and given the short timeframe, remains an open question.

When building DGVMs, it is perhaps inevitable to use plant functional traits. A range of issues are associated with measuring and using these traits, as discussed above. Traits do not necessarily correlate directly with relevant physiological processes, and they may not be useful in a process-based model. Furthermore, plant functional traits cannot be considered as constant for species across their whole geographical range and/or environmental gradients. A recent detailed analysis of how whole-plant traits covary with environmental conditions has been published by Patiño et al. (2012). One of the strongest correlations in their dataset was for the decline of sapwood density with increasing soil fertility (see also Fyllas et al. 2009), a relationship also known by foresters. A remarkable experiment has been conducted in the Brazilian cerrado to further explore this question (Bucci et al. 2006). By fertilising the soil for 36 months for five tree species, the authors showed that only the addition of nitrogen had a significant effect, and that nitrogen addition resulted in a decline in both sapwood density and in vulnerability to cavitation (the trees growing in an N-enriched soil had lower $P_{50}$ values than the controls). The study of Bucci et al. (2006) therefore suggests that most of the traits discussed here are either directly correlated to demographic variables (such as stem growth rate) or are intrinsically variable. This variability, together with the adaptive potential of tree species, cannot be overemphasised. Such trait–environment covariation has never been included in DGVMs, in spite of their obvious importance. More experimental and empirical results are needed before generalisations are possible on this front.

It would be desirable to implement a finer-grained description of tropical forest vegetation dynamics, allowing for a more accurate description of inter-specific and inter-individual variability. The problem raised here is one of parameter aggregation: it is often the case that by aggregating traits originally measured on individuals into a few discrete categories, the statistical properties of the entire dataset are altered. Although this problem has a remarkably long history in ecology (Iwasa, Andreasen & Levin 1987) and in forest model simulators (Hurtt et al. 1998; Ritchie & Hann 1997), it has been overlooked in recent attempts to develop DGVMs, in part owing to the lack of accessible databases on functional traits. One option for a new generation of DGVMs is to
develop individual-based versions to account for the physiological processes at play in tropical forest ecosystems. Only the outline of such an approach is presented here, based on a previous development of an individual-based spatially explicit forest growth simulator described in Chave (1999) and called TROLL. In the original version of this dynamic forest growth simulator, each tree with a trunk diameter of 1 cm or above is simulated. At most, one individual can occupy a grid cell of $1 \times 1$ m, thus allowing a maximum number of 10 000 individuals per hectare. Individuals compete for free cell space as in cellular automata (Hurtt & Pacala 1995), but they also compete for light resources. Solar radiation above the canopy may be computed from geometrical considerations of solar movement, and it may be decomposed into a direct and a diffuse component (Leuning et al. 1995; Monteith & Unsworth 2007). In agreement with the Beer–Lambert law, light intensity in a forest declines exponentially from the top of the canopy to the ground level (Hirose 2005). To model this light attenuation, I took a discrete approach whereby the leaf density is computed in each voxel of side 1 m within the canopy, assuming a turbid medium approximation within each voxel (Le Roux et al. 2001).

Death could result from a stochastic process, insufficient light availability (see also Pacala et al. 1996), carbon starvation (Fisher et al. 2010) or xylem embolism (Cochard 2006). The TROLL model also includes a detailed treefall gap formation module in which falling trees topple neighbours according to their relative height and size. Tree geometry is modelled explicitly by including, in addition to trunk dbh, total tree height, crown radius and crown depth. All of the parameters are defined for each species, hence there is no need to lump species into PFTs (but the intraspecific variability in ecological traits is ignored).

One challenge is to develop a leaf-level photosynthesis module averaged over sufficiently long time scales so as to avoid the issues of modelling the relationship between stomatal conductance $g_c$ to local environmental conditions (Lloyd & Farquhar 2008). This could be tackled by relating the mean ratio of intracellular to atmospheric CO$_2$ concentration, $c_i/c_a$, and carbon isotopic discrimination in leaves as modelled by $\delta^{13}C$ (Domingues, Martinelli & Ehleringer et al. 2007, 2010; Farquhar, Ehleringer & Hubick 1989). Indeed, carbon isotopic discrimination has been measured in a large range of trees empirically (Baraloto et al. 2010; Ometto et al. 2006). A second challenge is to include a detailed model of drought resistance, including the susceptibility of a plant’s leaves and of its water column to sudden droughts. Empirical data to model leaf drought tolerance remains scarce, as reviewed above, but empirical evidence relating basic wood properties such as sapwood density and resistance to xylem cavitation is now strong and convincing. Finally, this model poses a serious computational challenge, which has been a major impediment to the development of global individual-based DGVMs in the
past. To test this, I simulated the dynamics of a relatively small permanent plot (16 ha, 1 m spatial resolution). With these conditions, the TROLL model admits a maximum of 160,000 individuals at a time. Briefly, the test runs showed that species diversity can be maintained in the system while ecosystem variables (NPP, stem size distribution, biomass) reach an equilibrium within a few centuries. These results will be developed in a forthcoming work, but the point here is that such models are easily scalable using the impressive computer power available today. Importantly, they also offer an important means of performing direct and ecologically intuitive data assimilation.

To conclude, it is tempting to suggest that the oversimplification of plant functional types in existing DGVMs account, at least in part, for the predicted critical transition between forest and savanna in South America over the twenty-first century. Real ecosystems are species-rich, and some of their species (e.g. *Hymenaea courbaril* L.) thrive both in closed-canopy forests and in woodland savannas. Although they are scattered in the forest today, their fitness may be favoured by changing climates, and they would then rise to dominance in the decades to come. This floristic turnover, which cannot be modelled in the current generation of DGVMs, would help to maintain a closed canopy cover, and help minimise changes in ecosystem functions in the carbon, water and element cycles, and in the energy budget of the forest. Next generations of DGVMs should seek to bridge the divide between ecosystem science and community ecology, and account for biological diversity and for population processes.

**Acknowledgements**

This work is dedicated to the memory of Sandra Patiño. It is a pleasure to acknowledge the useful comments from C. Canham and an anonymous referee, and M. Chave for redrawing Figure 6.1. I benefited from enlightening discussions with C. Baraloto, M. Bartlett, D. Coomes, T. Domingues, T. Kursar, J. Lloyd, C. Lusk, H. Muller-Landau, C. E. T. Paine, L. Poorter, L. Sack, S. Schnitzer, M. Servant, S. Sitch, S. Thomas, I. Wright and A. Zanne. This work has benefited from Investissement d’Avenir grants of the ANR (CEBA: ANR-10-LABX-0025; TULIP: ANR-10-LABX-0041), and from grants from ANR Biodiversité (BRIDGE project), Fondation pour la Recherche sur la Biodiversité (ATROPHY project), and CNES (TOSCA Biomass).

**Appendix 6.1**

Compilation of values of xylem water potential at 50% loss of hydraulic conductivity ($P_{50}$) used to estimate the xylem vulnerability to cavitation, for tropical forest environments. Monocots, gymnosperms and mangrove species were excluded from this compilation.
<table>
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<tr>
<th>Species</th>
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<th>Country</th>
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Cecropia concolor Willd.  Urticaceae  Dry  −0.8  Bolivia  Markesteijn et al. (2011)
Ceiba speciosa (A. St.-Hil.) Ravenna  Malvaceae  Dry  −1.4  Bolivia  Markesteijn et al. (2011)
Centrolobium microchaete (Mart. ex Benth.) H.C. Lima  Fabaceae  Dry  −1.2  Bolivia  Markesteijn et al. (2011)
Guibourtia hymenaefolia (Moric.) J. Léonard  Fabaceae  Dry  −5.7  Bolivia  Markesteijn et al. (2011)
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Trichilia elegans A. Juss.  Meliaceae  Dry  −3.5  Bolivia  Markesteijn et al. (2011)
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<td>Brunei</td>
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<td>Baccaurea ramiiflora Lour.</td>
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<td>Bauhinia variegata L.</td>
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<td>Combretum latifolium Blume</td>
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<td>Millettia pachycarpa Benth.</td>
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<td>−3.2</td>
<td>Panama</td>
<td>Zotz et al. (1994)</td>
</tr>
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<td>−1.7</td>
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<td>Moist</td>
<td>−1</td>
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<td>Moist</td>
<td>−1.8</td>
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<td>Zotz et al. (1994)</td>
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<td>Pseudobombax septenatum (Jacq.) Dugand</td>
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