## <u>Ecology Letters</u>

Ecology Letters, (2014)

# REVIEW AND

### The enigma of the rise of angiosperms: can we untie the knot?

#### Abstract

L. Augusto,<sup>1</sup>\* T. J. Davies,<sup>2</sup> S. Delzon<sup>3,4</sup> and A. De Schrijver<sup>5</sup> Multiple hypotheses have been put forward to explain the rise of angiosperms to ecological dominance following the Cretaceous. A unified scheme incorporating all these theories appears to be an inextricable knot of relationships, processes and plant traits. Here, we revisit these hypotheses, categorising them within frameworks based on plant carbon economy, resistance to climatic stresses, nutrient economy, biotic interactions and diversification. We maintain that the enigma remains unresolved partly because our current state of knowledge is a result of the fragmentary nature of palaeodata. This lack of palaeodata limits our ability to draw firm conclusions. Nonetheless, based on consistent results, some inferences may be drawn. Our results indicate that a complex multidriver hypothesis may be more suitable than any single-driver theory. We contend that plant carbon economy and diversification may have played an important role during the early stages of gymnosperms replacement by angiosperms in fertile tropical sites. Plant tolerance to climatic stresses, plant nutrition, biotic interactions and diversification may have played a role in later stages of angiosperm expansion within temperate and harsh environments. The angiosperm knot remains partly tied, but to unravel it entirely will only be feasible if new discoveries are made by scientific communities.

#### Keywords

Angiosperms, biotic interaction, carbon, climate, diversification, evolutionary radiation, Gymnosperms, nutrient.

Ecology Letters (2014)

#### INTRODUCTION

For hundreds of millions of years, forests have represented a major type of ecosystems (Willis & McElwain 2002). The first tree species appeared in the late Middle Devonian Epoch (Frame 2003; Raven & Andrews 2010; Stein et al. 2012) and forests were originally dominated by giant lycophytes, sphenophytes and ferns, followed later by gymnosperm species (Willis & McElwain 2002; Crepet & Niklas 2009). While the exact date of their appearance is still debated, knowledge from fossils attests the presence of angiosperms since the mid-Early Cretaceous Period (Friis et al. 2010). At that time, angiosperm species were small plants which remained subdominant until the late Cretaceous Period (101-66 million years before present; see also Table S1 in Appendix S1 for a simplified chronology). Subsequently, angiosperms progressively came to dominate the majority of terrestrial ecosystems (Lidgard & Crane 1988; Willis & McElwain 2002; Crisp & Cook 2011), except in some forest ecosystems - mainly located at high latitudes or high altitudes - where conifers still dominate (Aerts 1995). Today, there are fewer than 1,000 extant gymnosperm species, among which conifers are the most abundant (Willis & McElwain 2002). The dramatic rise in the abundance of angiosperms around the world has been an enigma to biogeographers and evolutionary biologists. This almost

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<sup>2</sup>Department of Biology, McGill University, Canada <sup>3</sup>INRA, UMR 1202 BIOGECO, 33612, Cestas, France complete transition from a gymnosperm to an angiospermdominated flora remains unexplained. Many alternative hypotheses have been put forth to explain this major shift in vegetation composition during the Mesozoic and Cenozoic Eras (Bond 1989; Berendse & Scheffer 2009; Brodribb & Feild 2010; Labandeira 2010; Feild *et al.* 2011). All together, these explanations form a complex knot of competing theories.

We have reexamined the hypotheses that have been proposed to explain the ascent of angiosperms, and we have identified the traits which are likely to be important in facilitating the replacement of gymnosperms. The dominance of angiosperms within the global flora could be considered in terms of taxonomic diversity (i.e. the number of angiosperm species compared to other plant groups) or ecological abundance (i.e. the proportion of the total plant biomass of a given ecosystem constituted by angiosperm individuals). In this review, we have focused on the latter.

#### **GENERAL FRAMEWORKS**

A wide range of hypotheses can be found in the literature on the success of the angiosperms (Chabot & Hicks 1982). Explanations are frequently based on ecological or physiological innovations, functional traits or the emergence of positive nutritional feedback strategies. As pointed out by Mueller

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We pay particular attention to palaeodata, as these data provide direct evidence of the past. Advances in our understanding of vascular plant biogeography have been accelerated by the explosion in availability of fossil data and recent developments in historical biogeography (Knopf et al. 2012; Mao et al. 2012). These studies showed that gymnosperms are far from being conservative taxa that occupy narrow climatic and soil ranges. Moreover, living gymnosperms, the so-called 'living fossils', are significantly younger than previously thought (Crisp & Cook 2011; Nagalingum et al. 2011; Burleigh et al. 2012) and imperfectly represent species of the Cretaceous and Palaeogene Periods. Consequently, we used fossil data alongside information from phylogenetic trees depicting evolutionary relationships to unravel their palaeobiological past. We primarily used published chronologies of plant functional traits, climate and Earth environment to assess some frameworks. In addition, studies on modern species have been used to fill the many gaps in fossil data, assuming that they provide information on the functional traits of their ancestors. Current knowledge on gymnosperm species principally relies on conifers, and consequently analyses were sometimes simplified, focusing on comparisons between coniferous species (hence excluding cycads, ginkgos and gnetophytes) and angiosperm tree species. However, because conifers have resisted angiosperm expansion better than other lineages of gymnosperms, focusing on conifers might be misleading. In the final section, we discuss the implications of the possible pitfalls of using functional traits of modern conifers as a proxy.

#### The carbon framework

In the *carbon framework*, it is hypothesised that angiosperm species have outcompeted the formerly dominating gymnosperms through an improved ability to grow fast (Bond 1989; Coiffard et al. 2012). This increased growth rate in angiosperms has been related to a more efficient vascular hydraulic network because water transpiration is essential to the photosynthetic process (Brodribb & Feild 2010). Recently compiled data on plant fossils indicate that seed plants of the Jurassic Period (201-145 Myr.) had fairly low photosynthetic capacities (Brodribb & Feild 2010; Feild et al. 2011). These authors also report a sharp increase in the photosynthetic capacity of angiosperms during the Cretaceous period, around the Cenomanian Stage (101-94 Myr), whereas values for gymnosperms remained fairly constant, with the exception of Pinus needles (Brodribb & Feild 2008). The higher photosynthetic capacity acquired by angiosperm species therefore has been interpreted as a consequence of the densification of their vascular network in xylem and leaf tissues at this time (Brodribb & Feild 2010; Feild et al. 2011), which may have been especially profitable under contemporary atmospheric  $CO_2$  concentrations during that period (Mueller *et al.* 2010). The difference in size of the vessels and in xylem conductivity is still observed in modern tree species (Chabot & Hicks 1982; Maherali *et al.* 2004). In the *carbon framework*, the improved photosynthetic capacity of angiosperm leaves may have indirectly led to additional modifications of foliage necessary for high photosynthetic capacity, such as increased specific leaf area and leaf nitrogen (N) content (Reich *et al.* 1995).

It has been shown that modern angiosperm seedlings have a higher relative growth rate than coniferous gymnosperm seedlings (Cornelissen et al. 1996). The faster growth of angiosperm seedlings has been interpreted as a consequence of differences in functional traits involved in resource use, and linked to biomass partitioning and properties (Cornelissen et al. 1996; Comas & Eissenstat 2004; Warren & Adams 2005; Kuglitsch et al. 2008). Seedling growth rate of modern tree species thus supports the carbon framework. However, these observations are typical for seedlings growing in optimal conditions, and are inconsistent with surveys of mature trees in field conditions. Under natural field conditions, growth rates of conifers and angiosperms may be found to be similar (Aerts 1995; Reich et al. 1997), or higher (Downing & Weber 1984; Pretzsch 2009) for coniferous forests than for angiosperm forests in the same region. This contradiction between forest surveys and pot experiments may be explained by the fact that saplings and trees of evergreen coniferous species may have a higher leaf area index (LAI; m<sup>2</sup> of projected foliage surface per m<sup>2</sup> of soil) than deciduous angiosperms (Niinemets 2010) because there is a greater biomass of mature evergreen leaves at any one time (Chabot & Hicks 1982; Aerts 1995). Conifers are thus able to compensate for their low photosynthetic capacity with their high total leaf area (Chabot & Hicks 1982; Aerts 1995). In addition, in pot experiments, seedlings receive an unlimited supply of nutrients, light and water. Pot experiments are thus more focused on optimal growth than on effective growth. In an environment that is not scientifically controlled, plant growth is often limited by climate and soil fertility (Nemani et al. 2003; Elser et al. 2007), and effective growth values are notably lower than optimal values. The way a plant species is able to maintain its effective growth rate close to its optimum defines two theoretical groups of species (Chapin et al. 1993): low-resource species have low optimum growth rates but are efficient in maintaining their effective growth rate at a relatively high level in unfavourable environments, whereas high-resource species have higher optimal values, but lower effective growth rate values in unfavourable environments. Because most coniferous species are supposed to be low-resource species (Chapin et al. 1993), they may be able to compete with high-resource species (like many angiosperm tree species) in resource poor sites (Coley et al. 1985; Chapin et al. 1993).

To test this resource–growth interaction, we compiled growth data comparing angiosperm to gymnosperm tree species growing with a low, or a high level of available resources (i.e. nutrient and/or water availability). We used log ratios of the plant growth values (e.g. log[angiosperm:gymnosperm]). All details on methods and data sources are in Appendix S2. Although the number of case studies was not high enough for formal statistical analysis for all coniferous families (see Table S2), we revealed some interesting trends. We found angiosperms to have similar growth rates to conifers when resources are scarce (Fig. 1a). However, with increased availability of resources, angiosperm species tend to grow faster than coniferous species (Fig. 1a), probably because they are able to make better use of abundant resources compared to conifers (Fig. 1b). Our results are consistent with the theory of Chapin et al. (1993), and suggest that angiosperms are more competitive in productive habitats than conifers (Lusk et al. 2003). Our results also suggest that growth patterns are dependent on plant development stage. During the seedling stage, angiosperms may grow faster than conifers, whereas their ranking seems to be different at older stages (Fig. S2). This possible shift during the course of plant development highlights the functional differences between seedlings and mature plants (Cornelissen et al. 1996; Norby et al. 1999). This finding, if confirmed by further research, would also reconcile conflicting evidence between pot experiments and field surveys. Finally, our results suggest that high optimal growth rate of angiosperm seedlings is insufficient to explain the global expansion of angiosperm species, since the competitive ability of species relies on many plant functions at different developmental stages, for example, growth rate until seed production at the sapling stage (Cornelissen et al. 1996). This is especially true when the availability of resources is low, as may be the case in many in situ growing conditions (Grime et al. 1997; Nemani et al. 2003). The carbon framework may therefore apply in productive regions, such as rich soils in

(a) (b) 1.6 -Angiosperm : Gymnosperm ratio High resource : Low resource ratio 1.2 0.8 **Relative growth rate** 0.4 log[ratio] ) 0.0 B [\*\*\*] A [\*\*] Angiosperms Gymnosperms -0.4 -0.8 A [n.s.] B [(\*)] -1.2Low resource High resource

tropical climates, but other frameworks might be better at

explaining angiosperm rise in other harsher environments.

**Figure 1** Growth rates of angiosperm tree species vs. gymnosperm tree species. (a) growth ratio of angiosperm vs. gymnosperm. (b) growth ratios at high vs. low level of resources (nutrients and/or water). Values are log transformed (positive values indicate numerator > denominator). Boxplots (n = 18 case studies) followed by different uppercase letters differed significantly (P < 0.05; paired *t*-test). Symbols in square brackets indicate a mean value significantly different from 0 (*t*-test: \*\*\*, \*\*, \*, (\*) and n.s. indicate *P* value < 0.001, < 0.01, < 0.05, < 0.10 and  $\ge 0.10$  respectively). Method and references are given in Appendix S2.

-1.6 -

#### The climate framework

It has been proposed that the ancient gymnosperms could not tolerate a dry climatic niche, and thus the change of climate to drier conditions at the end of the Eocene could be responsible for the high extinction rates of the group (Crisp & Cook 2011). On the other hand, it has been frequently assumed that climate may have prevented angiosperms from becoming dominant in cool or cold environments because conifers are more frost tolerant than angiosperms (Enright & Hill 1995). A careful review of the literature partly showed evidence in support of both mechanisms.

The extinction of several conifer and cycad lineages at the end of the Eocene might have been caused by aridification. A recent study has shown that most, if not all, conifers of the Cupressaceae were not particularly drought tolerant before the end of the Eocene; the appearance of tolerant clades interestingly being concomitant with drier climatic conditions (Pittermann et al. 2012). Nevertheless, the change to a drier climate cannot explain why the Cheirolepidaceae became progressively extinct during the Upper Cretaceous and early Cenozoic (Friis et al. 2011). Indeed, this coniferous family was composed of species that were well adapted to warm and arid conditions, and had dominated the vegetation of large regions, at low and mid palaeolatitudes over long periods of time (Friis et al. 2011). The decline of the Cheirolepidaceae was synchronous with the initial rise in ecological abundance of angiosperms (Cretaceous Period; Table S1) and, consequently, could not be explained simply by a climate-related effect at the end of the Eocene. In addition, findings obtained on modern gymnosperms conflict with predictions of the *cli*mate framework related to water availability. Extant conifers intercept more rainwater than angiosperm species (Augusto et al. 2002), even during the growing season (Breda et al. 2006). This trait may modify environmental conditions (Westoby & Wright 2006) and directly reduce the amount of available water for plants (Breda et al. 2006). Consequently, coniferous forests may require higher precipitation than angiosperm forests. Assuming a similar drought tolerance in angiosperms and gymnosperms, this difference in water regime would support the water effect of the climate framework. We tested this possible water effect using drought resistance of current tree species. In practice, we compiled data from 587 tree species using the  $P_{50}$  parameter as a metric of plant drought resistance. The  $P_{50}$  parameter is the xylem pressure at which 50% of water conductivity is lost; very negative  $P_{50}$  values indicate high drought resistance. The resistance to cavitation is closely linked to drought-induced tree mortality (hydraulic failure) for both angiosperms (Urli et al. 2013) and conifers (Brodribb et al. 2010) and increases with increasing aridity (Maherali et al. 2004). Full explanations of methods and data sources are provided in Appendix S3. Our results showed that, contrary to the expected water effect, modern conifers exhibit evidence of higher drought resistance than angiosperms (Fig. 2). In addition, modern conifers generally maintain greater hydraulic safety margins than angiosperms (Choat et al. 2012). This buffer enables most conifers to withstand more negative water potentials, and therefore to maintain the integrity of their vascular systems during severe drought

events, compared to many angiosperms (Maherali *et al.* 2004; Choat *et al.* 2012). In sum, it seems that hydric factor may explain the rise to ecological dominance of angiosperms during some intervals of time, similar to the increasingly dry climate during the mid-Cenozoic, but not other time periods.

In the temperature link of the *climate framework*, conifers are supposed to be more resistant to freeze-thaw cycles than angiosperms. We tested this assumption by comparing angiosperms to gymnosperms in terms of xylem anatomy, because this trait strongly influences plant frost resistance (Davis et al. 1999). We compiled data on xylem from 301 tree species. More information on data and methods is available in Appendix S3. Results showed that xylem anatomy of modern species supports the assumption of conifers as being more frost resistant than angiosperms (Fig. 2). Indeed, embolism in the xylem occurs during thawing, when bubbles enclosed in the conduits expand, especially in wide conduits that contain large amounts of dissolved gas. Embolism formation upon freezing and thawing has been found to be minimal in extant conifers (Sperry et al. 1994; Davis et al. 1999; Feild & Brodribb 2001), except in cases of interaction with drought or in wide root xylem conduits (Mayr et al. 2007). The relatively high resistance of conifers to freeze-thaw stress is the result of two well-established observations: (1) the tracheids of conifers

are generally smaller than the xylem vessels of angiosperm trees (Chabot & Hicks 1982; Feild et al. 2011) and (2) the diameter of xvlem conduits is negatively correlated with vulnerability to freezing-induced cavitation [i.e. freeze-thaw stress (Davis et al. 1999; Pittermann & Sperry 2003)]. In practice, the global distribution of temperature is well associated with the modern biogeography of tree species (Enright & Hill 1995; Willis & McElwain 2002; Taggart & Cross 2009), with conifers being generally dominant in cold sites at high latitudes and altitude. Furthermore, this modern pattern seems applicable to geological times. At mid and high latitudes, conifers have experienced periods of ecological expansion and decline associated with cooling and warming events respectively (Taggart & Cross 2009; Brodribb et al. 2012). Similarly, it has been shown that the ecological expansion of angiosperms was delayed at higher latitudes and altitudes (Table S1), and involved three main evolutionary solutions permitting the colonisation of freezing habitats (Zanne et al. 2013): (1) some angiosperms species evolved a safe water transport system consisting of small-diameter vessels, (2) while others became deciduous by dropping their leaves during the freezing season, and (3) some took the option of becoming herbaceous. This general trend supports the assumption that low temperatures continuously have been a competitive advantage for conifers.



**Figure 2** Vulnerability to drought-induced cavitation (top panel) and to freeze-thaw (bottom panel) of extant angiosperm vs. gymnosperm tree species. Drought-induced cavitation is characterised by a vulnerability curve showing the variation of the percentage of cavitation as a function of xylem pressure potential. The accumulation of cavitation events during drought leads to plant death (Brodribb *et al.* 2010). Here, we reported the main parameter from this curve:  $P_{50}$ , the xylem pressure at which 50% of conductivity is lost. Freezing and thawing has been shown to increase the number of embolized xylem conduits, by measuring the maximum hydraulic conductivity of stem segments before applying stress, then immediately after a freeze-thaw treatment. The method and references are given in Appendix S3.

To conclude, the *climate framework* might explain how some gymnosperms, such as conifers, were able to resist the rise of the angiosperms in cold (at high altitude and latitudes in the Northern hemisphere) and dry environments (xeric woodlands in both hemispheres), but not how angiosperms were able to achieve an ecological advantage in warmer and milder environments. From this point of view, the *climate framework* remains compatible with the *carbon framework*.

#### The nutrient framework

Berendse & Scheffer (2009) have proposed a third hypothesis based on negative and positive feedback from nutrient cycling in ecosystems. In this hypothesis, conifers are supposed to be adapted to grow in soils with low nutrient resources (Chapin et al. 1993) and to keep their advantage by maintaining a low nutrient availability. Increased nutrient availability may thus be considered as a driver of the rise to dominance of angiosperms. Because not only the foliage but also the overall biomass of extant conifers have low nutrient contents (Chabot & Hicks 1982; Harmon et al. 1986; Aerts 1995), the loss of nutrients through litterfall and other necromass fluxes is much reduced (Aerts 1995). In addition, the long lifespan of evergreen conifer leaves is believed to be a possible evolutionary adaptation which enables an increase of the nutrient residence time in their foliage, further reducing the annual needs of nutrient uptake from the soil and the loss of nutrients through dead foliage (Rogers & Clifford 1993; Eckstein et al. 1999; Givnish 2002; Westoby & Wright 2006). This is the conclusion reached by Turner (1994) and Givnish (2002) from their reviews of sclerophylly, a property typically associated with conifers. According to Turner (1994), sclerophylly may be more likely to be the interactive consequence of nutrient shortages and water stress than water stress alone. The low nutrient content of necromass in conjunction with the high

lignin content (Harmon et al. 1986; Cornwell et al. 2008) also is supposed to strengthen the competitive advantage of nutritionally frugal species, like conifers, by reducing litter degradability, and as a result, creating negative feedback in the availability of soil nutrients. In the nutrient framework, disturbances in the ecosystem, which temporarily suppress the dominant vegetation, may have allowed the establishment of some angiosperm species thus generating a positive feedback. Angiosperm species produce litter which decomposes more easily and consequently nutrients are returned to the soil quickly. In this way, soil nutrient availability would be increased, providing an advantage to species with high potential growth rates (Grime et al. 1997), such as angiosperms (Chapin et al. 1993). Because most species able to fix atmospheric N<sub>2</sub> were angiosperms, in some cases, this may have indirectly facilitated the establishment of further positive nutritional feedback. In the nutrient framework, conifers have resisted angiosperm expansion in ecosystems at high latitudes or at high altitudes. This resistance is attributable to the low mean temperature which characterises these regions with bioavailable N-limited soils (Reich & Oleksyn 2004; Westoby & Wright 2006) that reduces N cycling, and hence N availability, to such an extent (Aerts 1997; Givnish 2002; Reich & Oleksyn 2004) that angiosperm species cannot become established to create positive feedback, even with symbiotic N<sub>2</sub> fixation (Givnish 2002; Houlton et al. 2008).

To evaluate evidence in support of the *nutrient framework*, we compiled data on nutrients cycling in current forest ecosystems. We identified the main processes and stocks involved in nutrient cycling and investigated the literature. We selected references which (1) compared quantitatively current angiosperm tree species to conifers and (2) were based on large datasets (review articles or meta-analyses). We used natural values of the angiosperm:gymnosperm ratio as the metric. Appendix S4 presents all methodological details about our



Figure 3 Nutrient cycling of angiosperms and gymnosperms tree species in forest ecosystems. Values are *angiosperm:gymnosperm* natural ratios for nitrogen, or nitrogen and phosphorus fluxes. Values above 1 indicate angiosperm > gymnosperm. Data were collected from review articles or meta-analyses (methods and references in Appendix S4) and are presented as ranges. Open box: aboveground nutrient flux (or nutrient pool); brown dashed box: belowground nutrient flux (or nutrient pool).

approach. As expected, our compilation suggests that angiosperm tree species may induce larger nutrient fluxes than conifers (Fig. 3). The annual demand for nutrients - and the flux of nutrients returning to the soil through litterfall - are substantially higher in angiosperm forests compared to coniferous forests. This result is consistent with the nutrient framework. The fact that current conifers are generally more abundant on nutrient-poor soils than on fertile soils (Enright & Hill 1995; Brodribb et al. 2012) is another argument supporting this framework. However, the nutritional feedback hypothesis remains incomplete. For example, nutrient resorption efficiency (the capacity of the plant to remove nutrients from foliage before senescence) is correlated with soil nutrient scarcity (Hayes et al. 2014). If nutrients were scarcer in soils supporting conifers than those of angiosperms, we could predict that resorption efficiency would be higher in the former. However, there is no obvious difference in resorption efficiency between conifers and angiosperms (Fig. 3). Moreover, biogeochemical data indicate only slightly faster nutrient cycling through belowground biomass and decomposition of soil organic matter in soils under angiosperms, compared to soils under conifers (Fig. 3). This latter result is important because a sharp difference in nutrient availability is assumed in this hypothesis, whereas only a small, inconsistent shift exists between angiosperms and gymnosperms (Mueller et al. 2010; Liu et al. 2014). To be plausible, the nutrient framework would also require conifers to dominate arctic N-limited ecosystems, which is not always the case. Therefore, our knowledge on extant tree species gives mixed support to the nutrient framework. We conclude that nutrients may have played an important role in the shift from gymnosperms to angiosperms during the Cenozoic Era with the expansion of eudicot species (Liu et al. 2014), but through interaction with other processes, such as climate and the carbon economy of plants.

#### The ecological framework

The *ecological framework* contends that angiosperms acquired new morphological innovations which, in the context of a particular environment, gave them a crucial advantage in terms of biotic interactions. Several hypotheses based on biotic interactions have been proposed to explain the past shift in the flora related to: (1) the consequences of herbivore pressure, (2) the seed production process and (3) the appearance of symbioses. We consider each in turn.

#### Herbivory

The palatability of the long-lived foliage of modern coniferous trees is known to be low (Chabot & Hicks 1982). This low level of palatibility is linked to scleromorphic properties such as thick leaves or thick cell walls (Turner 1994) and chemical composition, particularly low nutrient content or high content in C-based defences (Coley *et al.* 1985; Wardle *et al.* 2002) of their foliage. Under the herbivory hypothesis, the adaptative strategy of angiosperms was based on high growth but at the expense of high rates of biomass loss through herbivory. This accommodationist hypothesis assumes that a low level of defence may have been a successful strategy because it enables better use of opportunities for growth (Coley 1988), and hence

competitive superiority over species relying on high levels of defence but slow growth. Indeed, the consequence of some of the foliar properties associated with low levels of palatability is to reduce the photosynthetic capacity of sclerophyllous foliage (Chabot & Hicks 1982; Coley *et al.* 1985; Chapin *et al.* 1993) while increasing the construction cost of foliage (Chabot & Hicks 1982; Turner 1994), and hence to slow down plant growth. From this point of view, the herbivory hypothesis could be considered as a possible antecedent of other frameworks such as those based on plant carbon economy or nutrient economy.

#### Pollination and dispersal strategies:

Angiosperms are colloquially referred to as *flowering plants*, and it is thus logical that the acquisition of an elaborate reproductive organ such as the flower may help explain the success of the clade (Frame 2003). The angiosperm flower may have enabled (1) more efficient pollination because flowers are more attractive to pollinators (Friis *et al.* 2011), (2) more rapid production of seeds (Verdu 2002; Crepet & Niklas 2009) and (3) production of seeds attractive to disseminator animals, such as in fleshy fruits, all of which would have greatly enhanced dispersal potential (Janzen & Martin 1982). These key innovations could have given a decisive advantage to angiosperms in the race for ecological dominance.

#### Symbioses

Both symbiotic N<sub>2</sub> fixation and mycorrhizae are related to nutrition (Raven & Andrews 2010), with the former exclusively related to N supply, and the latter to increased soil exploration for water and nutrients. Symbiotic N<sub>2</sub> fixation is an association observed in some modern angiosperm families. While the majority of modern coniferous trees in the Northern boreal realm have ectomycorrhizal (ECM) fungi, most angiosperms are associated with arbuscular mycorrhizal (AM) fungi (Brundrett 2002). Forests with AM tree species are generally characterised by faster nutrient cycling (Phillips et al. 2013), while ECM fungi provide the ability to access nutrient pools that are inaccessible to AM fungi (Taylor et al. 2009). These differences could also support the nutrient framework in the sense that ancient gymnosperms were on average more adapted to nutrient-poor sites (Berendse & Scheffer 2009). Such symbiotic relationships may therefore have given a crucial competitive advantage to angiosperms.

In practice, it is difficult to evaluate the relevance of these different hypotheses quantitatively, but we can propose some qualitative assessments. In the herbivory hypothesis, the palatable foliage of angiosperms results in high herbivore pressure (Coley 1980; Wardle *et al.* 2002) compared to conifers (Coley *et al.* 1985; Farrell 1998), but because growth rate is not significantly elevated in mature angiosperm trees (Fig. S2 in Appendix S2), the predicted trade-off is only partly met. Moreover, the construction cost of evergreen foliage does not appear to be very different from that of deciduous foliage (Aerts 1995), whereas this difference is often presented as a key argument of the herbivory hypothesis. On the whole, the herbivory hypothesis does not appear to be strongly supported by current knowledge, but deserves further investigation.



Figure 4 Chronologies of acquisition of some ecological innovations in angiosperms and gymnosperms. Solid lines, dashed lines and dotted lines indicate confirmed, probable and possible presence, respectively, of a given innovation. Grey background areas are used to distinguish different geological periods (Devonian, Carboniferous, etc.). Question marks indicate an uncertain date of appearance. Data were collected from articles listed in Appendix S5.

The hypothesis based on dispersal strategies of pollen and seeds has some valuable arguments, but also some drawbacks. On one hand, many angiosperms of the Cretaceous were not pollinated or had their seeds dispersed by biotic processes (Wing & Boucher 1998; Friis et al. 2011). Furthermore, recent work indicates that gymnosperms were actively pollinated by specialised insect species and had used different types and modes of pollination since at least the late Early Jurassic (Fig. 4). The fact that some insect species were engaged in pollination mutualisms with some gymnosperms questions the importance of pollinator mutualism in explaining the success of angiosperms via reproductive innovations (Willis & McElwain 2002; Friis et al. 2011; Penalver et al. 2012). Similarly, some gymnosperms of the Mesozoic (i.e. Bennettitales, Cycadales, Ginkgoales) had fleshy fruits, and consequently were probably dispersed by zoochory (Friis et al. 2011). The Bennettitales and Cycadales had reproductive structures with many morphological similarities to flowers (Willis & McElwain 2002), but these elaborate structures did not prevent these groups from becoming extinct (Bennettitales) or decreasing in speciosity (Cycadales) while the Coniferales, characterised by simple reproductive structures, were able to better resist the ecological expansion of angiosperms (Willis & McElwain 2002). Finally, early lineages of angiosperms had only small simple flowers which were unlikely to attract exclusive relationships with insect pollinators (Friis et al. 2011). Large and/or sophisticated flowers appeared relatively late (Friis et al. 2011) and consequently might not be the cause of the first stages of the ecological rise of angiosperms. Similarly,

most of the insect diversification occurred relatively late, during the Palaeogene period (Crepet & Niklas 2009), also suggesting that plant-insect relationships were not strongly involved during the first stages of ecological rise. All in all, the flower, the defining feature of angiosperms, does not seem to be the only cause explaining the ecological expansion of angiosperms. On the other hand, the intense diversification of insects associated with the entire Palaeogene period (Labandeira & Sepkoski 1993; Crepet & Niklas 2009) suggests that angiosperms had flowers which were effectively more attractive to insects and thus pollinators, than did gymnosperms of those times. The relatively early appearance of most modern floral characters is consistent with this assumption (Crepet & Niklas 2009; Friis et al. 2011). Based on this mixed set of evidence, and following Labandeira (Labandeira et al. 2007; Labandeira 2010), we suggest that the efficiency of angiosperm pollination may have played an important role, but in interaction with other drivers.

As for the case of angiosperms flowers, symbioses are unlikely to be the single driver of their ecological success. First, despite the imbalance in the distribution of AM and ECM symbioses in seed plants (see above), recent studies indicate that mycorrhizal fungi were associated with angiosperm and gymnosperm tree species during the Cretaceous: for the AM, the *Podocarpaceae* (Brodribb *et al.* 2012), and for the ECM, the *Fagaceae* (Brundrett 2002; Taylor *et al.* 2009). Even if *Pinaceae*, the most abundant of extant conifers, principally harbour ECM symbioses, the majority of coniferous tree species have AM symbioses (Enright & Hill 1995). Moreover, the acquisition of these biological innovations by conifers occurred before the rise of angiosperms (Fig. 4). Available data about mycorrhizal symbioses are thus non-discriminatory. Associations involved in atmospheric  $N_2$  fixation of rhizobial symbiosis and actinorhizal symbiosis provide a more plausible explanation because these mutualisms are found almost exclusively in angiosperm clades (Berendse & Scheffer 2009). However, the symbiotic  $N_2$  fixation process is not likely to be used intensively by plants in temperate biomes (Houlton *et al.* 2008), where angiosperm species are abundant. Similarly, the acquisition of rhizobial symbiosis and actinorhizal symbiosis probably occurred relatively late (Fig. 4), and these ecological innovations cannot explain the early stage of expansion of angiosperms at low palaeolatitudes (Table S1).

To conclude, no single biotic interaction appears to be able to explain the shift in vegetation from a gymnospermous to an angiospermous flora. However, it is likely that some of these relationships made a significant contribution to the resource-use strategy adopted by angiosperms, such as nutrients required to produce fleshy and attractive fruits (Givnish 2010), or the recruitment of new plant individuals through effective pollination and dispersal strategies.

#### The diversification framework

The rise to ecological dominance of the angiosperms was marked by a rapid diversification of several key lineages that now encompass much of present-day angiosperm species richness. Although present-day species richness is a product of much more recent diversification events, reconstructed estimates suggest that some basal lineages may have had high net rates of diversification (Davies et al. 2004). This rapid early diversification of angiosperms in the Albian, approximately 113-101 Myr ago, is thought to be reflected in the poor phylogenetic resolution of many of these early diverging lineages within early molecular studies using few genes, which were confounded by the short times between diversification events, as there was little opportunity for mutations to accumulate (Soltis et al. 1999). The rise to ecological dominance was therefore accompanied by a rise in numerical dominance in species diversity as early angiosperm lineages diversified (Wing et al. 1993). The diversification framework suggests that the success of the angiosperms may be linked to the increase in the production of new lineages through an increased rate of phylogenetic branching that represented a diversity of form and function, and thereby the potential to occupy new and diverse niches. While gymnosperms were more species rich in the past, their maximum richness never approached that observed for current angiosperms.

Absolute diversification rates of angiosperm families vary by more than one order of magnitude (Magallon & Sanderson 2001), and have likely changed over time (Davies *et al.* 2004). These rate shifts may be too frequent to be simply explained by one or a few key traits that allowed entry into new adaptive zones (Crepet & Niklas 2009). Shifts in rates might therefore more reflect changes in climate or biogeochemical conditions that favoured the radiation of some lineages over others at different times in the evolutionary past (Davies & Barraclough 2007). Thus, as the environment changed, so did the identity of rapidly diversifying lineages, which were those pre-adapted to diversify under the new environmental regime. With greater species richness, came a greater opportunity for ecological success. The diversification framework thus assumes that species-rich lineages would have a greater chance of containing a species that could adapt first to a new environment. In essence, the diversification framework contains all other frameworks, because it is based on the assumption that high species richness enables a lineage to include species characterised by individuals with high levels of fitness in terms of growth, resistance and dispersion. While high net diversification rates can be explained by either high speciation and/or low extinction, here we have placed greater emphasis on speciation because of the observation of increasing angiosperm species richness over time (Willis & McElwain 2002).

The single best predictor of species richness among angiosperm lineages is the size of geographical range; clades occupying larger areas have more species and faster diversification rates (Davies et al. 2005; Vamosi & Vamosi 2010). Although it is difficult to infer whether large geographical extent facilitates further diversification, or if high species richness allows clades to occupy greater geographical areas, the link between area occupied and species richness supports a scenario of ecological diversification associated with lineage diversification. The geographical expansion of the angiosperms may therefore have been tightly linked with their evolutionary diversification, although many species might still have maintained relatively narrow geographical extents. It is now more widely recognised that angiosperms expanded their geographical range and diversified before they came to dominate terrestrial ecosystems (Table S1). Thus, the shift in dominance occurred at a time when angiosperms were already widespread and highly diversified. This chronology supports the hypothesis that the rise to dominance of angiosperms might not have a simple explanation linked to any one trait, but to different traits such as pollination mode, or lifestyle (Davies et al. 2004) that may have been important at different times and in different locations. It is this diversity that might best explain their success.

Currently, quantitative tests of the diversification framework are difficult because (1) approximately half of probable angiosperm species are still unrecorded [this gap is sometimes referred to as the Linnean shortfall (Brown & Lomolino 1998)], and (2) until recently, a lack of rigorous statistical methods to evaluate diversification rate shifts associated with the evolution of the geographic ranges of species. Recent advances in methods (Goldberg et al. 2011) hold much promise, and offer the potential to evaluate the link between the geographic expansion and diversification rate shifts directly, one step towards testing the diversification framework. However, the great species richness of flowering plants remains a major challenge for the application of such tools. In addition, there is a critical need to generate more comprehensively sampled phylogenetic trees. Advances in next generation sequencing methods show promise in providing greater genetic sampling, although this must be accompanied by equal efforts

aimed at sampling unknown taxa to address the *Linnean* shortfall. Current knowledge suggests that extinction rates, rather than low speciation rates, account for the lower extant diversity of gymnosperms (Friis *et al.* 2005; Crisp & Cook 2011; Leslie *et al.* 2012), perhaps indicating that the radiation of the angiosperms might have had the greatest impact on now extinct families at low latitudes. Therefore, while the *diversification framework* may have played a role during the rise of angiosperms, because the potential for rapid diversification might have provided angiosperms with more chances to exploit new opportunities, it is unable to explain the replacement of gymnosperms at high latitudes.

#### THE ANGIOSPERM GORDIAN KNOT

Our interpretation of the world around us is commonly based upon our own preconceptions and biases. Faced with the enigma of the rise to dominance of angiosperms, different communities of scientists have tended to look inwards for an explanation. Tree physiologists mainly consider plant growth or resistance to different types of stress; biogeochemists emphasise plant nutrition and nutrient cycling; whereas ecologists tend to focus on biotic interactions. Studying the rates of diversification of angiosperms, Davies et al. (2004) suggested that no simple scenario based on a few key innovations was consistent with observations. Diversification was better explained by complex interactive effects of biological traits and the environment. In the same way, we show that almost no simple theoretical framework fully explains the ecological rise of angiosperms. Only diversification might, in itself, provide a theoretical framework able to solve the problem. However, this framework lacks quantitative support, and further dedicated studies are required.

We suggest that current knowledge is insufficient to achieve a final resolution, specifically due to limited palaeodata. Addressing the shift in dominance from a gymnosperm to an angiosperm-dominated flora is extremely complex because the environment (i.e. climate, soils, etc.), composition of communities, and values of functional traits have all changed continuously in space and over time (Wing & Boucher 1998). Consequently, information from extant species can only provide one piece of the puzzle. Current gymnosperms are not living relicts: most modern species appeared relatively recently, during the Cenozoic (Crisp & Cook 2011; Burleigh et al. 2012); so, to understand the past we must also consider the lineages with no extant descendents. Because current gymnosperms are, by definition, descendants of lineages which did not become extinct, they are imperfect analogues of gymnosperms of the Cretaceous and the Palaeogene. The decline of conifers, for instance, was mainly confined to the extinct Cheirolepidiaceae family (Brodribb et al. 2012). Similarly, other coniferous families experienced an intense species turnover during the Late Cretaceous and the Cenozoic (Taggart & Cross 2009; Friis et al. 2011) and thus modern conifers do not necessarily represent the Mesozoic conifers (Penalver et al. 2012). Finally, it is important to note that most of our knowledge about gymnosperms is based on conifers. Nevertheless, conifers were generally better at resisting the ecological rise of angiosperms compared to other

gymnosperms (Willis & McElwain 2002). The ecological expansion of the angiosperms was thus at the expense of lineages for which modern conifers may be a poor proxy. For example, at least some of the Cheirolepidiaceae conifers, Bennettitales, Cycadales and Ginkgoales were insect pollinated (Labandeira et al. 2007; Crepet & Niklas 2009; Penalver et al. 2012). Due to the scarcity of exhaustive chronologies of environmental change, diversification and the acquisition of functional traits, attempts to unravel the history of the rise of angiosperms might seem a hopeless endeavour. There probably are many links among these numerous variables, and it may be difficult to determine which of two correlated variables modifies the other (Frame 2003; Westoby & Wright 2006), with some variables demonstrating a correlation without having a causal relationship (Maherali et al. 2004; Crepet & Niklas 2009). Efforts to aggregate the different explanatory frameworks (Figures S1a to S1e) into one unified scheme result in an inextricable knot (Fig. S3 in Appendix S1). Like the famous Gordian knot of Greek legend, our challenge is to untie the knot by determining the causal factors, rather than understanding how its components are interlinked, or how their relationships are identified. Indeed, the qualitative network of relationships between the different processes is now quite well established. What is missing is knowledge of the pattern of causality (Wing & Boucher 1998; Clarke et al. 2011) and the quantitative contribution of the different factors. As has been suggested (Chabot & Hicks 1982; Crepet & Niklas 2009; Brodribb et al. 2012), there is probably more than one answer.

Even if, without exhaustive chronologies, it is almost impossible to describe all the events that led to the rise to dominance of angiosperms, we can make several well-supported inferences. First, angiosperm species initially were restricted to low latitudes (Table S1). If, as suggested by available fossils, angiosperms were mainly present in fertile alluvial sites characterised by nearly optimal conditions for plant growth (i.e. tropical climate, nutrient-rich substrates), it would imply that the carbon and diversification frameworks are good candidates as the main drivers (alone or in interaction) of the initial expansion of angiosperms in these non-limiting environments. The fact that species in the Podocarpaceae evolved broad flattened leaves (Biffin et al. 2012; Brodribb et al. 2012), resulted in more light efficient and shade tolerance under the productive canopy-forming angiosperms of tropical forests (Brodribb & Hill 1999), suggests that the *carbon framework* may be prominent in tropical ecosystems.

Later during the Cretaceous period, the ecological dominance of angiosperms spreads towards higher latitudes (Table S1) – or altitudes – and to less fertile sites (Wing & Boucher 1998). In this secondary expansion stage, the *climate*, *nutrient*, *ecological* and *diversification frameworks* were probably important. In less competitive environments, conifers probably persisted well, due to their ability to resist low temperatures and nutritive stresses. The modern distribution of conifers and cycads is consistent with this scenario, as they are frequently found on nutrient-poor soils (Waring & Franklin 1979; Binkley & Giardina 1998; Lusk & Matus 2000). Following Wing & Boucher (1998), we suggest that the change of climate to hot-dry conditions after the Palaeocene may have brought about the expansion of angiosperm domination by pushing conifers to higher latitudes and altitudes (Willis & McElwain 2002; Taggart & Cross 2009). The cooler-wetter climates which succeeded to this dry period may explain the later resurgence of conifers at lower latitudes and altitudes (Willis & McElwain 2002; Taggart & Cross 2009), especially on nutrient-deficient soils, or in dry lands for the lineages newly adapted to water stress (Pittermann et al. 2012). The most obvious contemporary examples are the Northern boreal forests, where frost resistance probably provides *Pinaceae* conifers with a decisive advantage over angiosperms (Taggart & Cross 2009). The considerably smaller area occupied in the Southern Hemisphere by extant Cupressaceae, Podocarpaceae and Araucariaceae is consistent with their lower frost resistance and with warmer temperatures in this region (Enright & Hill 1995; Taggart & Cross 2009; Brodribb et al. 2012).

Finally, grass species have reinforced angiosperm dominance since the Miocene Epoch in many ecosystems where trees were unable to dominate, as in very cold or dry environments. Indeed, even if the first grasses probably appeared somewhat earlier, their ecological abundance remained quite low before the Miocene Epoch (Willis & McElwain 2002). Before the rise of grasses, it remains unclear, however, to what extent non-woody angiosperms contributed to the expansion of their lineage. In this study, we focused principally on trees, as they represent an important proportion of plant fossils (Willis & McElwain 2002), and because they can compete better for light acquisition than herbaceous species. However, the relative role of herbaceous angiosperms vs. woody angiosperms during the expansion of their lineage needs to be quantified.

In summary, some hypotheses are unable to explain why the angiosperms became dominant. Such are the case of hypotheses relying on herbivory or symbioses. In addition, no one simple framework (except perhaps the diversification framework, which is not discussed further) is sufficient to explain the shift from a gymnosperm-dominated to an angiosperm-dominated flora. Rather, the different frameworks must be considered together, with their relative importance varying over space and time: the carbon framework and, to a lesser extent, the pollination-dispersal hypothesis have probably played a continuous role, but of decreasing importance with decreasing temperature and nutrient availability. The climate and the nutrient frameworks have probably assisted angiosperms to become dominant during certain periods, such as the dry period of the Cenozoic, and in certain sites characterised by a sufficient level of nutrient availability. If the climate and the nutrient frameworks help to explain how angiosperms have become dominant in some regions, they also provide a plausible explanation for the continuing prominence, or dominance, of conifers in cool to cold environments, especially on poor soils. In addition, some coniferous species may have maintained a significant abundance as a result of major ecological disturbances that include wildfires, landslides and floods; here, conifers may have avoided competition with angiosperms via long-lived individuals which were able to induce large recruitments of seedlings

following disturbances that suppressed angiosperm dominance (Lusk & Ogden 1992; Duncan 1993; Enright & Hill 1995; Brodribb *et al.* 2012). This regeneration strategy is not inconsistent with the *carbon framework*, or with the *nutrient* or *climate frameworks*, as it supports the idea that angiosperms outpace conifers if environmental conditions are not too stressful. However, the fact that not all conifers avoid competition with angiosperms (Enright & Hill 1995; Brodribb *et al.* 2012) illustrates the complexity when explaining the shift in vegetation to an angiosperm-dominated community based on a single, simple ecological process. Current knowledge indicates that a multidriver hypothesis is more suitable at explaining the rise of angiosperms than any single-driver theory.

Although we illustrate that many frameworks are at least partly supported by empirical data, they remain theoretical explanations. In the absence of complete chronologies, we are still unable to untie the knot of the angiosperms enigma completely. The Greek legend has it that, faced with the impossibility of untying the Gordian knot, Alexander the Great solved the problem by cutting through it with a sword. We believe that consolidating the data regarding modern plant biogeography, plant traits, climate and the nutritional status of soils could help to quantify the relative importance of several of the processes addressed here. We propose that an improved understanding of modern plant biogeography may represent the first cut in the knot. Because modern data are available, this rough approach might be instructive in the short term. In the long term, only new palaeodata - and significant advances in the fields of plant ecophysiology and phylogeny - might enable the scientific community to untie the knot of the angiosperms enigma.

#### ACKNOWLEDGEMENTS

We sincerely thank Nathalie Nagalingum for her relevant comments on the whole manuscript, and particularly on the diversification framework. We thank Filip Ceunen for his help during the design of some graphs and Mark Bakker, Florian Delerue, Mathieu Fortin and André Schneider for their fruitful advice, and encouragement. Our gratitude also goes to Sylvie Jeanloz and Aldyth Nys who have helped us in reviewing the manuscript. We finally thank five anonymous referees whose comments have greatly improved this study.

#### STATEMENT OF AUTHORSHIP

LA initiated the project. LA and ADS decided the structure of the first draft of the manuscript, and LA wrote it. All authors contributed substantially to the revisions. In particular, TJD contributed to the diversification framework, SD to the climate framework and ADS to the carbon, the nutrient and the ecological frameworks.

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Editor, Jerome Chave Manuscript received 28 February 2014 First decision made 2 April 2014 Second decision made 26 May 2014

Manuscript accepted 10 June 2014