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SPECIAL FEATURE

THE TREE OF LIFE IN ECOSYSTEMS

Understanding the ecosystem implications of the angiosperm rise to dominance: leaf litter decomposability among magnoliids and other basal angiosperms

Guofang Liu[1]†, William K. Cornwell[2,7]†, Xu Pan[1,3], Kunfang Cao[4,5], Xuehua Ye[1], Zhenying Huang[1], Ming Dong[1,6]* and Johannes H. C. Cornelissen[2]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [2]Systems Ecology, Department of Ecological Science, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands; [3]Graduate University of Chinese Academy of Sciences, Beijing 100049, China; [4]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China; [5]College of Forestry, Guangxi University, Nanning 530004, China; [6]College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 310036, China; and [7]School of Biological, Earth and Environmental Science, University of New South Wales, Kensington 2052, Sydney, Australia

Summary

1. Litter decomposition has been a key driver of carbon and nutrient cycling in the present and past. Based on extant species data, there is a great deal of variation in litter decomposability among major plant lineages, suggesting potential shifts in plant effects on carbon and nutrient cycling during the early evolutionary history of angiosperms.

2. Existing data suggest that eudicot species produce faster decomposing litter compared to gymnosperms, ferns and mosses. One of the missing puzzle pieces in this transition is the basal angiosperms, the functional role of which in past carbon and nutrient cycling has seldom been investigated. We hypothesized that owing to constraints on leaf and plant design related to hydraulic capacity, basal angiosperm trees should generally have resource conservative leaves of low decomposability and that fast-decomposing leaves may only be found in short-statured taxa.

3. We performed a litterbag experiment with simultaneous outdoor incubation of leaf litters in a common environment, including 86 basal angiosperm species (including the magnoliid lineage), 33 eudicots, five gymnosperms and four ferns. We fit a nonlinear model to the decomposition data, and each species' decomposability was estimated using the proportional rate of mass loss through the experiment.

4. The mass loss rates were 59.2% lower in basal angiosperms than in eudicot trees. There was one exceptional group within basal angiosperms: the Piperales had higher k values than other magnoliid lineages, but all of the free-standing species were short. Eudicots had higher k values overall and covered a range of plant statures from small-statured herbs to big woody trees.

5. *Synthesis*. Understanding the ecosystem-level effects of the angiosperm rise to dominance is a crucial goal. Our results indicated that, among generally slow-decomposing magnoliid lineages, only the Piperales have fast decomposition rate associated with small plant statures. Thus it is unlikely that early magnoliid trees were both forest canopy dominants and produced resource acquisitive leaves turning into fast decomposable litter during the evolutionary history of angiosperms.

Key-words: ancestral character state estimation, basal angiosperm, character diversification, evolution, growth form, leaf litter decomposability, magnoliids, Piperales, plant–soil (below-ground) interactions

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*Correspondence author: E-mail: dongming@hznu.edu.cn

†Equal first authors.

Introduction

Decomposition of organic matter derived from plant litter is an important ecosystem flux. The rate of litter decomposition drives fluxes of both carbon and the macro-nutrients important for plant growth (Swift, Heal & Anderson 1979; Coûteaux, Bottner & Berg 1995; Chambers *et al.* 2000; Aerts 2006; Tuomi *et al.* 2009). Interspecific variation in the structure and chemistry of leaf litter has a large magnitude effect on decomposition rates (Cornwell *et al.* 2008), which often vary by more than 10-fold among species even within climate zones and ecosystems. This species-based variation in decomposability is not evenly spread across the phylogeny of land plants: gymnosperm litter decomposes about 44% slower than eudicot litter on average, and ferns and bryophytes produce even slower decomposing litter (Cornwell *et al.* 2008). This observation has led to some inference about the role of decomposability in past ecosystems, as it affects both nutrient cycling (Berendse & Scheffer 2009) and ground fire frequency (Bond & Scott 2010; Bond & Midgley 2012). Moreover, it may also have had major direct effects on carbon cycling in the past.

On average, extant gymnosperms are characterized by low mass-based photosynthetic and respiration rate, nitrogen and phosphorus content and specific leaf area but long leaf life span comparable to eudicot angiosperms (Reich *et al.* 1998; Lusk, Wright & Reich 2003; Wright *et al.* 2004), implying an absence of gymnosperms at the fast end of leaf economics spectrum (Reich *et al.* 1995; Cornelissen, Castro-Diez & Carnelli 1998; Freschet *et al.* 2010). In contrast, a large proportion of the eudicots are at the fast end of this economics spectrum with a resource acquisition strategy when compared with the resource conservation strategy that predominates among gymnosperms. The direct evidence from fossils also hints at a gymnosperm – angiosperm difference in leaf traits: specific leaf area was higher in angiosperm fossils relative to those from gymnosperms (Royer *et al.* 2010).

The evolutionary innovations associated with the rise of angiosperms is an area of intense research interest, and the connections between hydraulic innovations and their influence on leaf traits are key to such innovations. Some new-found fossil records showed that leaf hydraulic capacities of angiosperms rose as atmospheric CO_2 concentration declined (Beerling & Franks 2010). In angiosperms, leaf venation and large numbers of small stomatal pores also represent innovations in leaf physiology, enabling transpiration and photosynthesis rates higher than those of their predecessors (Beerling & Franks 2010; Brodribb & Feild 2010; Feild *et al.* 2011; de Boer *et al.* 2012). Angiosperm hydraulic capacity was promoted with accompanying large shifts in body size, wood hydraulic efficiency and vein density (Feild *et al.* 2011; de Boer *et al.* 2012).

These hydraulic traits are coordinated with leaf traits in important ways (Sack, Tyree & Holbrook 2005; Brodribb, Feild & Sack 2010; Poorter *et al.* 2010; Westoby, Cornwell & Falster 2012). As a canopy dominant, exposed to full sun, leaves need extensive hydraulic support and leaf-level photosynthetic investment to achieve a fast rate of photosynthesis (Brodribb & Jordan 2011; Peltoniemi, Duursma & Medlyn 2012). This problem is especially acute among forest canopy dominants where hydraulic investment per unit whole-plant conductance is large (Franks 2004; Westoby, Cornwell & Falster 2012). This positive feedback mechanism coupled with a shift in leaf hydraulic capacity (Beerling & Franks 2010; Brodribb & Feild 2010; Feild *et al.* 2011; de Boer *et al.* 2012) could be one of the vital mechanisms to unravel why angiosperms rose to dominance across much of the globe at the end of the Cretaceous (Feild *et al.* 2011; de Boer *et al.* 2012). This innovation may also have had profound implications for the structure and chemistry of the leaves as determinants of the decomposability of the litter derived from them.

There has been relatively little research on the decomposability of basal angiosperm lineages. The very limited data within Cornwell *et al.* (2008) suggested that decomposability within the magnoliid lineage is comparable to that in eudicots, implying that highly decomposable leaves could have been present in these lineages, but this was based on only 21 species, meaning that any consideration of the transition from slowly decomposing gymnosperms to fast-decomposing eudicots is still strongly constrained by a lack of data.

Basal angiosperms often have low hydraulic transport capacity such as low leaf vein density, primitive vessels or tracheids relative to eudicots (Sperry 2003; Sperry *et al.* 2007; Feild, Chatelet & Brodribb 2009), or, as in the Piperales, by limited secondary cambial growth (Isnard *et al.* 2012). These constraints on leaf hydraulic architecture seem to be linked with a resource conservative strategy (sensu Díaz *et al.* 2004; Wright *et al.* 2004) of magnoliid leaves. Indeed, Cornwell *et al.* (2014, this issue) showed that magnoliid leaves generally have greater mass per area and, presumably therefore, greater toughness than those of eudicots. As such, we hypothesized that most lineages of basal angiosperms would have traits consistent with a location at the conservative, 'slow return' end of the plant and leaf economics spectrum with leaves associated with slow relative growth rate and low decomposability once dead. A consequence of this hypothesis based on hydraulic and mechanical constraints would also be that any basal angiosperm lineages with a resource acquisition strategy, that is, with 'fast return' leaves, should be short in plant stature. Owing to structural and chemical 'afterlife effects' of their poorly reinforced, fast return leaves, such lineages should have relatively fast leaf litter decomposition (Cornelissen *et al.* 2004).

To provide a conclusive test of which, if any, basal angiosperm lineages (especially in the magnoliids) have quickly decomposable leaves, and whether these would then coincide with relatively short plant stature, we conducted a 'common garden' decomposition experiment (sensu Cornelissen 1996) with simultaneous incubation of leaf litters of 128 species, contrasting basal angiosperm lineages with eudicots, gymnosperms and ferns. We consider the decomposability data from this experiment in the light of both the phylogeny and data on species stature.

Materials and methods

STUDY SITE, LITTER COLLECTING AND PHYLOGENY

Fieldwork was conducted in Xishuangbanna Tropical Botanical Garden (XTBG), Menglun, Yunnan province, China (21°55′38.03″N, 101°15′54.87″E). The climate in XTBG is mainly influenced by the south-west monsoons with alternating dry and wet periods; annual mean precipitation is 1463 mm, 85% of which falls during the summer monsoon season (Li *et al.* 2012). A number of basal angiosperms, such as Nymphaeales, Schisandraceae, Chloranthaceae and magnoliids, are common in this region. XTBG hosts a wide representation of many of the major extant basal angiosperm lineages in the (subtropical and tropical parts of the) world.

In total, 128 species were used in the leaf litter decomposition experiment including 86 species of basal angiosperms, comprised of Nymphaeales, Schisandraceae, Chloranthaceae, Piperaceae, Saururaceae, Lauraceae, Myristicaceae, Magnoliaceae and Annonaceae. Twenty species of ferns and gymnosperms and 22 eudicots, partly from the temperate forest zones where an important portion of their present-day distribution is, were also included (Fig. 1, left panel). The gymnosperms and eudicots were all woody so as to justify direct comparison with basal angiosperms, the predominant lineages of which were also woody. The species identification of each individual (labelled and bar-coded) plant we collected litter from had been verified and where needed updated by expert taxonomists. Higher level nomenclature followed the Angiosperm Phylogeny Group III (Bremer *et al.* 2009; see below). The leaf litter collections for (sub)tropical forest species (including virtually all of the basal angiosperm species) at XTBG were done in April and May 2011 and leaf litter of a smaller subset of (mostly eudicot) species was collected from temperate forests and gardens in the Beijing region in autumn 2010. In XTBG, management included watering during the dry period. In addition, the soil had low pH and phosphorus availability (Cao 2009). We took particular care to always collect recently senesced, undecomposed leaf litter without substantial herbivory or pathogen damage (Cornelissen 1996), either by shaking trees or branches, gently brushing along branches with our fingers or by picking up individual leaves from the soil surface. Leaf litter collections of each species were stored air-dry in paper bags until further processing.

In estimating phylogenetic relatedness, there is a trade-off between species coverage and accurate branch length estimation: first, we used two trees at different points on this trade-off surface. A backbone phylogenetic tree was built based on the online software Phylomatic (Webb & Donoghue 2005) based on the APG III consensus topology, and branch lengths were estimated using simple assumptions. Secondly, we used a recently published phylogeny of 31 749 angiosperm species (Tank *et al.* 2013). This phylogeny was generated using a maximum likelihood approach based on molecular data for seven loci (18S, 26S, ITS, matK, rbcL, atpB and trnLF), constrained based on both several recent phylogenetic systematic treatments of seed plants and fossil dates for major clades. The phylogenetic tree can be found in Dryad Digital Repository (Burleigh *et al.* 2010, 2011) and at http://www.onezoom.org/forreview4819537841/plants.htm. This tree contained 71 of all 128 species in the decomposition data set.

DECOMPOSITION EXPERIMENT

Approximately 1.5 g of litter of each sample per species was preweighed to and carefully placed in litterbags with 1 × 1 mm mesh size; this presumably allowed access by some but not all detritivorous soil fauna (Bradford *et al.* 2002). Litterbag dimensions were 15 × 10 and 25 × 15 cm to accommodate small and large leaf sizes, respectively, without damage. Very large leaves were cut into several segments to fit inside litterbags without further damage to the tissues. At the time of litterbag filling, a subsample was taken for moisture correction of initial dry weight; these subsamples were weighed air-dry, then oven-dried (at 65 °C for 48 h) and reweighed. The litter decomposition experiment, based on the approach of Cornelissen (1996), was conducted in an experimental incubation bed (7 × 7 m) at XTBG, in an open experimental garden partly shaded by surrounding trees. The bare brick-red loamy soil (oxisol), cleared of weeds, was covered with a thoroughly mixed litter matrix containing surface leaf litter (with predominance of *Camellia oleifera*, *Mangifera indica*, *Litchi chinensis*, *Hevea brasiliensis*, *Artocarpus heterophyllus* and mixed bamboo spp.) collected from several woody stands in XTBG. We acknowledge that interactions between litter type (species) and the litter environment in terms of climate and soil parameters, and associated decomposers, may be important (e.g. Swift, Heal & Anderson 1979; Vivanco & Austin 2008; Ayres *et al.* 2009). However, large studies where multiple species were incubated in highly contrasting litter beds in terms of climate and soil/litter matrix have shown that such interactions between species decomposition rates and incubation environment tend to be of small effect size compared to overall species rankings (Cornelissen *et al.* 1999, 2007; Freschet, Aerts & Cornelissen 2012; Makkonen *et al.* 2012).

Then the litterbags were laid on the first layer of this leaf litter matrix in three randomized blocks (of 6 × 1.5 m each), with one replicate per species per harvest time in each block. Finally, litterbags were covered by a second layer of this litter matrix to prevent sunlight exposure and to buffer against desiccation. Considering the generally fast decomposition rates in the tropical climate locally, without major drought, the experiment lasted 1 year from 17 May 2011 until 17 May 2012. Litterbags were harvested after 1, 3 and 12 months, respectively. There was negligible visible damage to litterbags by termites. The content of the litterbags was gently brushed clean, and litter was dried at 65 °C for 48 h and weighed. Litter decomposition rate of a sample was determined by dividing litter mass loss after 1, 3 and 12 months by its initial dry mass, respectively. Additionally, maximum heights of the sampled species were obtained from the Flora of China and the Yunnan Flora of China (ECCAS 1974–99; Wu 1977–2006).

DATA ANALYSIS

In a few replicates, we observed a slight mass gain, likely due to debris falling into the litterbag. In these cases, we set mass loss at zero. We carried out nonlinear least square regressions using the nls function in R (R Development Core Team 2012) to determine the exponent *k* and its standard error in Olson's (1963) negative exponential decomposition model ($Y_t = Y_o e^{-kt}$). As there was no significant difference in litter decomposition rate among the three blocks ($F_{2,373} = 1.84$; $P = 0.160$), we used all nine data points (3 blocks × 3 harvests) for each species to conduct the curve fitting for obtaining *k* values. Dichotomized APG III phylogenetic trees were created using the multi2di function in the *ape* package in R. Ancestral character states for *k* values in leaf litter decomposition were estimated by means of the *ace* function of the *ape* package in R, according to the phylogenetic tree including ferns, gymnosperms, basal angiosperms (Nymphaeales, Schisandraceae, Chloranthaceae, Piperales, Magnoliales and Laurales) and eudicots. Moreover, a similar procedure was carried out based on an available molecular phylogenetic tree. One-way

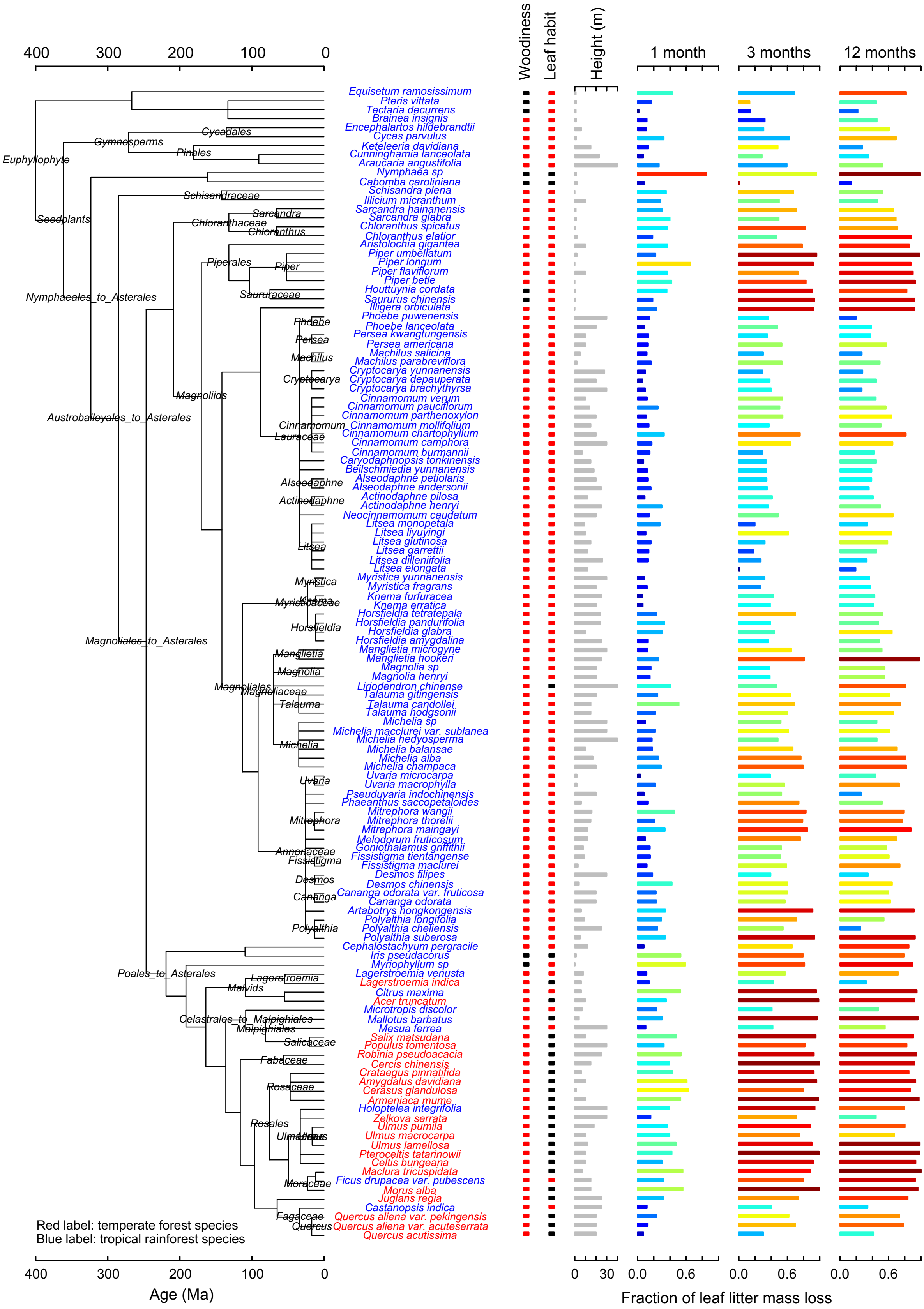

Fig. 1. Phylogenetic position of tropical rain forest species (blue labels, left column) and temperate forest species (red labels), and woodiness, leaf habit and fraction of leaf litter mass loss (representing decomposability) after 1, 3 and 12 months in the tropical litter incubation bed (three right columns). Red versus black bars denote woody versus herbaceous habit for woodiness and evergreen versus deciduous leaf habit, respectively. The fraction of leaf litter mass loss gradually increased from dark blue, via yellow, to dark red bars.

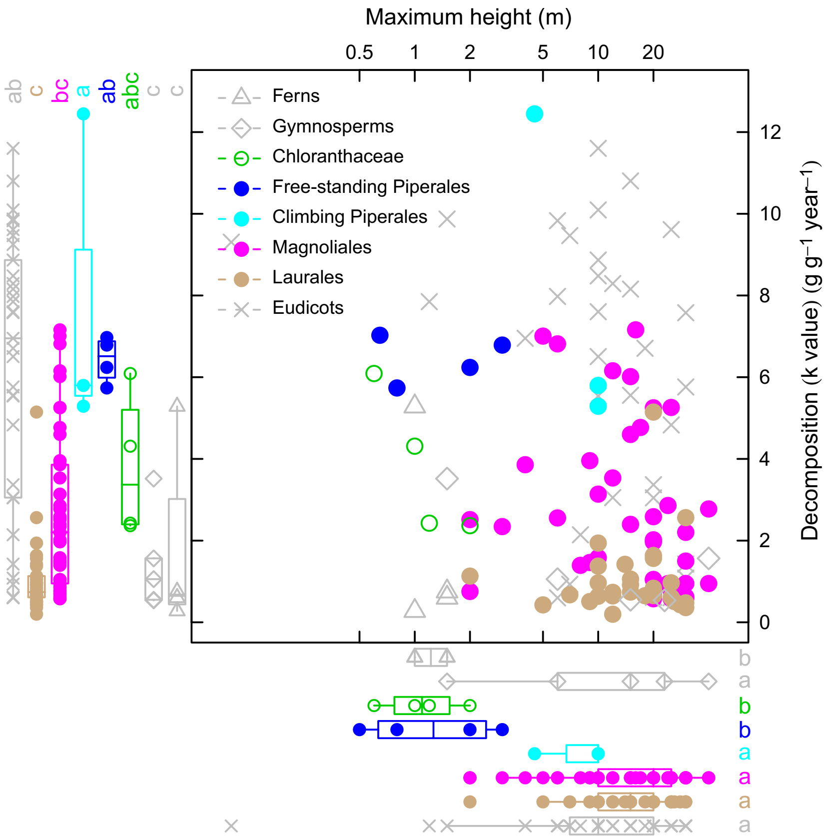

Fig. 2. The scatter plot and box-and-whisker plots of *k* values representing leaf litter decomposability, and maximum height, of plants across ferns, gymnosperms, Chloranthaceae, Piperales, Laurales, Magnoliales and eudicots. Basal angiosperms are highlighted with coloured filled (magnoliids) and empty circles to contrast with the other clades with grey symbols. The same lowercase letter for *k* values or maximum heights denotes non-significant difference between different phylogenetic groups. There was a significant overall negative correlation between *k* values and maximum height of basal angiosperm species ($R^2 = 0.09$, $P < 0.001$).

ANOVAs were used to test the influences of those lineages on *k* values in litter decomposition and maximum heights of those species, followed by Tukey's honest significant differences (Tukey HSD) tests. Ordinary least square (OLS) regression was used to uncover the relationship between maximum heights and *k* values of basal angiosperm species. All statistical analyses were conducted in R2.15.0.

Results

The basal angiosperms exhibited a wide range of leaf litter decomposition rates (Fig. 1), but the mean *k* value was far lower than that for eudicots (2.52 ± 0.26 versus 6.18 ± 0.59 g g^{-1} $year^{-1}$). Basal angiosperms had an average *k* value as low as those in the ferns and gymnosperm clades (Fig. 2). Within magnoliids, free-standing and climbing Piperales had relatively large *k* values and they were smaller statured plants as compared with the Magnoliales and Laurales (Fig. 2). Also, the *k* values in the Chloranthaceae lineage, also associated with small stature, appeared larger than those in the Magnoliales and Laurales lineages and smaller than those in the Piperales lineage, but these apparent differences were not significant possibly due to their small sample sizes (Fig. 2). Within basal angiosperm species, the *k* values were negatively correlated with maximum height ($R^2 = 0.09$, $P < 0.001$).

Results from the ancestral character state estimation for *k* values in litter decomposition were similar no matter which phylogenetic tree (AGP III or molecular phylogenetic trees) was used (Fig. 3, Fig. S1 in the Supporting Information). Ancestral character state estimation showed that the basal angiosperms possessed relatively low *k* value compared with the eudicot clade within this tropical, moist litter bed environment ($k = 4.6$ versus 5.3 g g^{-1} $year^{-1}$, Fig. 3). In addition, decomposition rate increased within the Piperales lineage departing from the core magnoliid clade that generally had relatively lower *k* values (see Figs 1 and 2). The Piperales and Nymphaeales lineages shared larger *k* values of 5.5 and 9.3 g g^{-1} $year^{-1}$, respectively.

Discussion

In contrast to previous results, leaf litter decomposability was on average low in the magnoliid clade when compared with the woody eudicots. Within the magnoliid lineage, slow-decomposing litter may be explained by green leaf traits exerting strong after-life effects on leaf litter decomposition due to tougher structure (Pérez-Harguindeguy *et al.* 2000) as well as high contents of secondary compounds that inhibit decomposition (e.g. aromatic leaves in the genus *Cinnamomum*). Berendse & Scheffer (2009) proposed a positive feedback whereby angiosperms with their higher growth rates profit more rapidly from increased nutrient supply than gymnosperms, while at the same time angiosperms promote soil nutrient release by producing litter that is more easily decomposed; this might have aided the rise of angiosperms at the end of the Cretaceous. This main result suggests that the magnoliid clade is not a strong candidate lineage for part of the hypothesis put forward by Berendse & Scheffer (2009) – it is

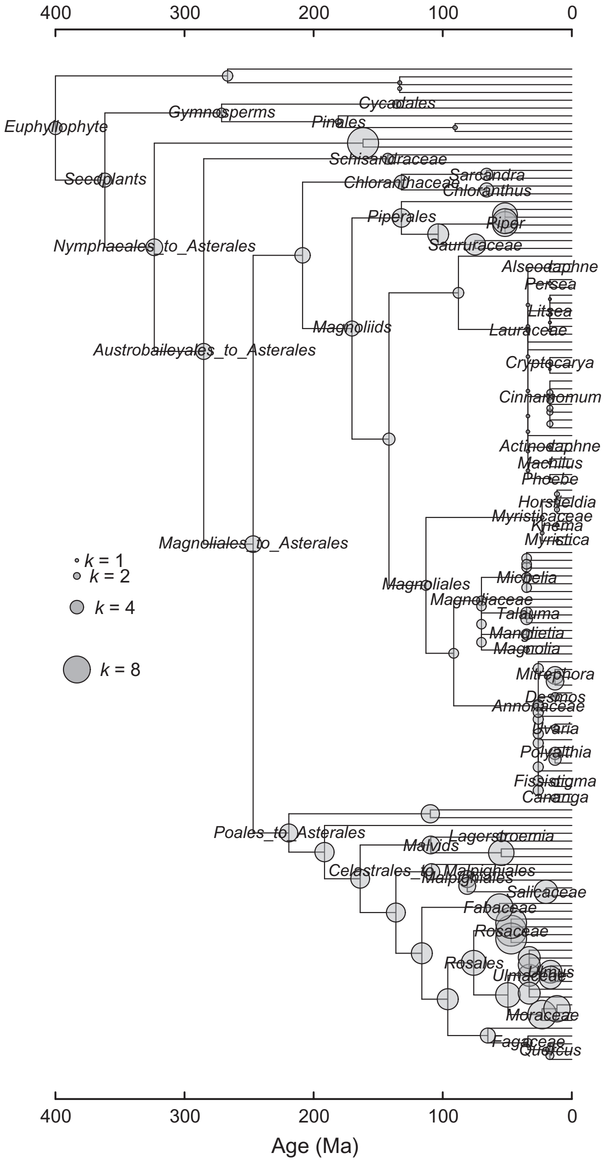

Fig. 3. Ancestral character state estimation of *k* values (g g^{-1} $year^{-1}$) in an exponential decay model of leaf litter decomposability in basal angiosperms based on the APG III phylogenetic tree. The sizes of the grey circles denote the *k* values of the nodes based on ancestral character state estimation. Tip labels of the phylogenetic tree were omitted in order to highlight the pattern of ancestral states of litter decomposition (but see in the left panel of Fig. 1 for tip labels of the phylogenetic tree).

unlikely that during the evolutionary history of angiosperms, there were early magnoliid trees that were both forest canopy dominants and produced resource acquisitive leaves turning into fast-decomposing litter. First, the magnoliid clade that does produce fast-decomposing litter, the Piperales (see Fig. 1), does not show this trait in combination with tall height growth and free-standing stems (Fig. 2). Secondly, there are a few examples of free-standing trees with fast-decomposing litter within the Magnoliales, but these are embedded within a larger clade that generally produces slow-decomposing litter, and reconstruction methods suggest that a fast-decomposing ancestor is very unlikely (Fig. 3). Thus, with respect to this hypothesis and to any potential major shifts in ecosystem flux rates, the eudicots is a more likely lineage to have evolved this combination of traits.

Mueller *et al.* (2010) formulated a conceptual framework that both climate (through evolutionary advances in leaf-gas exchange, hydraulic architecture and stomatal sensitivity) and nutrient availability could have promoted the rise of angiosperms against gymnosperms. If we extend this hypothesis to evolutionary lines within the angiosperms, there may be a complex, but crucial, relationship between hydraulic capacity, leaf traits and their effect on decomposability within the basal angiosperms and the magnoliids. Extant species from basal angiosperm lineages feature very low vein density and hydraulic capacity in general (Beerling & Franks 2010; Brodribb & Feild 2010; Feild *et al.* 2011; de Boer *et al.* 2012). Interestingly, species in the eudicot lineage could appear in any place within the two-dimensional space comprising plant height and litter decomposition (Fig. 2) perhaps because this clade has evolved multiple trait combinations to support resource acquisition and conservation strategies for environments varying greatly in productivity and disturbance regimes (Díaz *et al.* 2004; Wright *et al.* 2004). Surprisingly, there were no species with higher decomposability and tall tree stature in both Magnoliales and Laurales lineages. Poor hydraulic capacity (Beerling & Franks 2010; Brodribb & Feild 2010; Feild *et al.* 2011; de Boer *et al.* 2012) may be a potential explanation for this pattern: a well-developed ability to transport water to the canopy is crucial for allowing stomata to remain open during times of high vapour pressure deficit. With a reduced ability to transport water to the canopy efficiently (relative to eudicots), it may not be feasible or useful to produce high N, fast-photosynthesizing leaves and associated fast-decomposing litter (Feild & Wilson 2012).

Piperales is an especially interesting clade with very diverse growth forms represented including many understorey and vine species (Jaramillo, Manos & Zimmer 2004; Isnard *et al.* 2012). Free-standing species have the added demands of building stems that function as both structural support and hydraulic transport, and that requires a more complex hydraulic architecture and secondary cambial growth (Isnard *et al.* 2012). As such, the connections between hydraulics and leaf traits (high hydraulic efficiency and relatively low carbon investments of stems being associated with acquisitive, fast-turnover leaves) represent a link between growth form and litter decomposition differences (Zhang & Cao 2009; Santiago 2010).

The rise of angiosperms to dominance has been of massive interest to many scientists since Darwin first highlighted this major shift in vegetation composition and function (Pellmyr 1992; Crepet 1998; Berendse & Scheffer 2009; Butler *et al.* 2009; Friedman 2009; Soltis *et al.* 2009; Vamosi & Vamosi 2010). There is abundant evidence that angiosperms, on average, produce leaves that decompose faster than gymnosperms (Cornwell *et al.* 2008), with many potential implications for ecosystems (Bond & Midgley 2012). Here, we have added a much finer resolution picture of that shift towards fast decomposability. While especially the Piperales clade evolved ‘acquisitive’ leaves turning into highly decomposable litter, the major magnoliid clades are predominantly recalcitrant to decomposition, and thus, the big switch from generally low gymnosperm decomposability to much greater decomposability in angiosperms depends strongly on the evolution of eudicot leaves. Fully understanding the global rise to dominance of angiosperms requires investigation of the traits that facilitated the angiosperm rise as well as the ecological and biogeochemical implications of that rise. As such, our approach of linking evolutionary history with litter decomposability, as derived from experimentation on ecosystem effect traits of extant species, bears much promise for application to past carbon and nutrient cycling contributions of other clades. For instance, monocots would be a particularly interesting clade in this respect, including the carbon and nutrient cycling consequences of Poaceae (grasses and bamboos), which have expanded into a very successful clade world-wide. Another extension of our approach will be to apply it to understanding contributions of vegetation composition to past fire regimes, by combining phylogeny to experimental testing of the flammabilities of multiple extant species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Ancestral character state estimation of k values in an exponential decaying model of leaf litter decomposability.