META ANALYSIS

Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs

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ABSTRACT

Aim Recent meta-analyses have revealed that plant traits and their phylogenetic history influence decay rates of dead wood and leaf litter, but it remains unknown if decay rates of wood and litter covary over a wide range of tree species and across ecosystems. We evaluated the relationships between species-specific wood and leaf litter decomposability, as well as between wood and leaf traits that control their respective decomposability.

Location Global.

Methods We compiled data on rates of wood and leaf litter decomposition for 324 and 635 tree species, respectively, and data on six functional traits for both organs. We used hierarchical Bayesian meta-analysis to estimate, for the first time, species-specific values for wood and leaf litter decomposability standardized to reference conditions (k^*_{wood} and k^*_{leaf}) across the globe. With these data, we evaluated the relationships: (1) between wood and leaf traits, (2) between each k^* and the selected traits within and across organs, and (3) between wood and leaf k^*.

Results Across all species k^*_{wood} and k^*_{leaf} were positively correlated, phylogenetically clustered and correlated with plant functional traits within and across organs. k^* of both organs was usually better described as a function of within- and cross-organ traits, than of within-organ traits alone. When analysed for angiosperms and gymnosperms separately, wood and leaf k^* were no longer significantly correlated, but each k^* was still significantly correlated to the functional traits.

Main conclusions We demonstrate important relationships among wood and leaf litter decomposability as after-life effects of traits from the living plants. These functional traits influence the decomposability of senesced tissue which could potentially lead to alterations in the rates of biogeochemical cycling, depending on the phylogenetic structure of the species pool. These results provide crucial information for a better representation of decomposition rates in dynamic global vegetation models.

Keywords

Coarse woody debris, decomposition, forest ecology, hierarchical Bayesian models, leaf economics spectrum, litter, meta-analysis, plant functional traits, wood traits.

INTRODUCTION

Decomposition of leaf litter and dead wood has an important impact on nutrient cycling and fluxes of carbon (C) from the land to the atmosphere (Swift *et al.*, 1979; Aerts, 1997; Berg & McClaugherty, 2008; Wirth & Lichstein, 2009). While leaf litter tends to decay faster than wood litter, it is poorly known whether species with rapidly decaying leaf litter also have rapidly decaying wood. Understanding how decomposition rates vary across different plant organs and in relation to variations in functional traits is of vital importance for predicting how future global changes may affect C and nutrient cycles via biotic feedback mechanisms (Chapin *et al.*, 2009; Brovkin *et al.*, 2012).

Decomposition rates are controlled by climatic variation, primarily of temperature and humidity, across biomes (e.g. Berg *et al.*, 1993; Moore *et al.*, 1999; Chambers *et al.*, 2000). Within biomes, plant functional traits, particularly those associated with plant strategies for resource acquisition or defence, explain much of the residual variation in decomposition rates (Chambers *et al.*, 2000; Cornwell *et al.*, 2008; Weedon *et al.*, 2009). Higher nitrogen and phosphorus concentrations are associated with more rapid decay (e.g. Melillo *et al.*, 1982; Berg *et al.*, 1993; Aerts, 1997), whereas organs having higher concentrations of recalcitrant structural C compounds (e.g. lignin) decay more slowly (Moore *et al.*, 1999; Cornwell *et al.*, 2008). While most past studies focused on nutrient concentrations in the litter to predict decay rates, it has been shown that nitrogen and phosphorus concentrations of living leaves and wood (N_{leaf}, N_{wood} and P_{leaf}, P_{wood}, respectively) also predict decay rates (Santiago, 2007; Freschet *et al.*, 2012). High specific leaf area (SLA) and low tissue density can directly speed up litter decay via a high surface-to-volume ratio and fragility or indirectly via their correlation with the aforementioned chemical properties (Quested *et al.*, 2007; Bakker *et al.*, 2011). Similarly, increasing wood density (ρ_{wood}) can decrease wood decomposition rates directly through reduced resistance to fragmentation and decomposer colonization (Chambers *et al.*, 2000) or indirectly through effects on wood moisture content and oxygen supply (Chambers *et al.*, 2000; Chave *et al.*, 2009). Maximum tree height (h_{max}) may act on wood decay rates via associated biomechanical properties such as wood strength, which prevents tall trees from collapsing (Niklas, 1992).

A key question to understanding ecosystem-level decomposition rates and C storage is whether the traits of living tissue driving wood and leaf litter decomposition rates are linked across species. Most leaf traits that influence decomposability vary in a predictable and coordinated fashion along trade-off axes between acquisitively and conservatively constructed leaves, i.e. the leaf economics spectrum (LES; Grime, 1979; Reich *et al.*, 1997; Wright *et al.*, 2004). Conservative leaves are characterized by relatively low foliar nutrient concentrations, low rates of photosynthesis and growth and correspondingly slow returns on carbon and nutrient investment. Acquisitive leaves are relatively nutrient replete, have higher processing rates and faster returns on investment. A wood economics spectrum (WES; Chave *et al.*, 2009) is likely to exist as well, but trade-offs within

a WES are less well understood than those of the LES. Furthermore, the few quantitative investigations of relationships and coordination between wood and leaf traits have yielded few generalizations (Wardle *et al.*, 1998; Wright *et al.*, 2007; Baraloto *et al.*, 2010; Freschet *et al.*, 2010). Cross-species correlations between wood and leaf trait axes across an assemblage of sub-arctic plants (Freschet *et al.*, 2010) reflected a single axis of variation in decomposability of the different organs (Freschet *et al.*, 2012). Conversely, Baraloto *et al.* (2010) found no correlation between wood and leaf trait spectra across 668 tree species of the tropical rain forest. Little is known about how tightly wood and leaf nutrient concentrations are related, and it remains unclear how wood and leaf traits interact across vegetation types at a global scale.

The two primary goals of our study were to test for a potential correlation between wood and leaf litter decomposability across tree species globally, and to assess whether this relationship is mediated by different wood traits and traits captured by the LES. We compiled two global datasets of wood and leaf litter decomposition rates for 324 and 635 species, respectively. Furthermore, we compiled a trait matrix of 1480 species for six plant functional traits known to drive biogeochemical cycling (SLA, N_{leaf}, P_{leaf}, leaf habit, ρ_{wood} and h_{max}). In a subset of 149 species used for trait analysis we also included two important wood chemical traits (N_{wood} and P_{wood}) which were unavailable for the full trait matrix of 1480 species. Our data allowed evaluation of the relationships between decomposability and functional traits within leaves or wood as well as between the organs. We hypothesize that: (1) wood and leaf litter decomposability can be predicted from wood and LES traits of living tissues at the global scale (Fig. 1a); and (2) wood and leaf litter decomposability are correlated if wood and LES traits are coordinated (Fig. 1b); alternatively, no correlation of wood and leaf litter decomposability is expected if wood and LES traits are unrelated (Fig. 1c).

MATERIALS AND METHODS

Data sources for wood and leaf litter decomposability and related traits

We searched Web of Science and the non-primary literature (theses, reports) for publications reporting decomposition rates of wood and/or leaf litter (see Appendix S1 in Supporting Information for bibliographic references). The majority of studies presented decomposition data in terms of fitted values of *k*, the decay constant in the single negative exponential decay model (Olson, 1963). In other cases, we used reported mass- or density-loss data to calculate *k*. Although widely used both historically and currently, the single negative exponential decay model is a drastic oversimplification of the decay process and can lead to inaccurate extrapolations whenever actual mass loss deviates from the assumed first-order dynamics (Harmon *et al.*, 2009). However, expressing decomposability in terms of *k* allowed the maximal use of available decomposition data, as more realistic models require larger datasets than those commonly generated (but see, e.g., Harmon *et al.*, 2009). We discuss
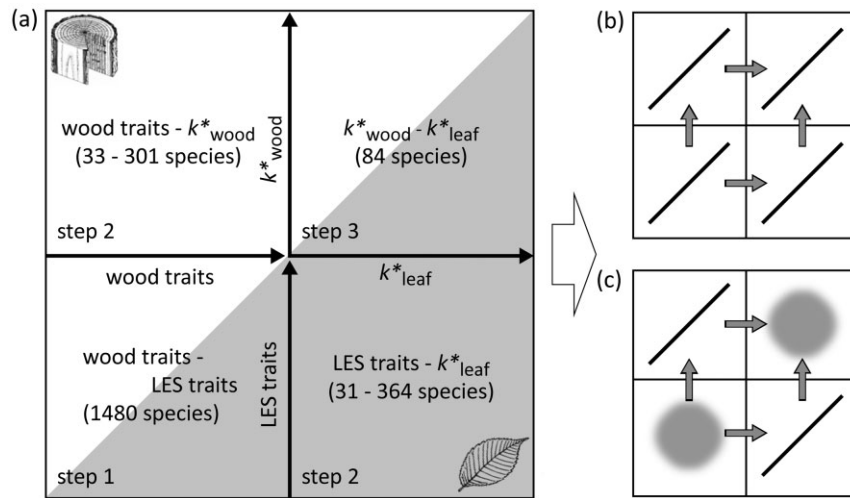
Figure 1 (a) General approach to relate the relationships between wood traits and leaf traits (associated with the leaf economics spectrum, LES) to the decomposability of dead wood and leaf litter ($k^\star_{wood}$ and $k^\star_{leaf}$, respectively). Step 1 involves exploring the coordination of wood and LES traits. Step 2 is confirmatory and tests whether links between wood and LES traits and wood and leaf litter decomposability, respectively, may serve a logical 'transfer function' for the dataset at hand. Step 3 tests whether the correlation pattern of wood and LES traits is reflected in the correlation pattern of $k^\star_{wood}$ and $k^\star_{leaf}$. (b) In this framework correlation of $k^\star_{wood}$ and $k^\star_{leaf}$ is predicted when wood and LES traits are correlated and jointly span a gradient between conservative and acquisitive species. (c) No correlation of $k^\star_{wood}$ and $k^\star_{leaf}$ would arise when this is not the case.

the implications of this choice for interpreting our results in more detail below (see Discussion).

Leaf litter decomposition data were restricted to woody species and included needle leaved, evergreen and deciduous species. We discarded data collected under aquatic conditions (i.e. in rivers and wetlands), and where data sources included experimental treatments (e.g. fertilization, CO_2 enrichment) we only used the data from unmanipulated controls. Data on k were recorded as mean values at the level of species, site and study.

For every k value, we recorded available key metadata, including location (i.e. latitude, longitude and elevation), the approach to quantifying decomposition (experimental or chronosequence) and methods. For leaves, the methodological covariates included duration of decomposition, mesh size of the litterbags, number of harvests, irrigation regimes (irrigated prior to the experiment or not), position (buried or not buried), contact of litter samples with soil type (mineral soil, topsoil or surface litter) and possibility for root in-growth (yes or no). For wood, the methodological covariates included duration of decomposition, soil contact status (yes or no), initial diameter of log or stem and the basis of observation (mass or density). Finally, for each location, we obtained estimates of mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) from a global climate dataset (WorldClim; Hijmans *et al.*, 2005). These data were incorporated in the meta-analysis models to standardize decomposition rates to mean climatic and methodological conditions.

In total, we compiled wood decomposition data for 324 species from 91 studies and leaf litter decomposition data for 635 species from 116 studies (built on data by Cornwell *et al.* (2008) for leaves, and Weedon *et al.* (2009) and an unpublished

database of C.W. for wood). Eighty-four species were associated with both wood and leaf litter decomposition data (the overlap dataset). The decomposition datasets span all forested climate zones (Appendix S2).

Meta-analysis of wood and leaf litter decomposition

We conducted a hierarchical Bayesian meta-analysis (HBMA) (Ogle *et al.*, 2013) to estimate standardized species-specific decomposition rate constants ($k^\star$) for wood and leaf litter. This approach allows us to account for the influences of methodological, climate and study effects. The extraction of decomposition information from the literature resulted in incomplete reporting of the covariates, an issue common to many studies involving analysis of literature-derived data. The HBMA approach was specifically designed to avoid an unrealistic influence of missing covariate data on k-related parameters by treating missing values as stochastic. This procedure allowed us to greatly expand the datasets of Cornwell *et al.* (2008) and Weedon *et al.* (2009) as we were not restricted to multispecies studies within a given climate zone or site. We highlight the most important components of the HBMA by focusing on the leaf $k^\star$ model: $k_{leaf,i}$ denotes the leaf decomposition rate (year^{-1}) reported for observation i [$i = 1, 2, \ldots, 1002$ (1409 for wood)]. We assumed that log ($k_{leaf,i}$) is normally distributed around a (log-scale) mean ($\mu_{leaf,i}$) that depends linearly on all methodological and climatic covariates. We parameterized the model with the temperature dependency following a Q_{10}-type response, where the Q_{10} parameter describes the multiplicative change in (regular-scale) k_{leaf} for a 10 °C change in MAT. We included a MAP by MAT interaction to account for the possibil-

ity that the Q_{10} value depends on water availability. We allowed the covariate effects to vary between biomes and taxonomic groups (tropical angiosperms versus temperate/boreal gymnosperms versus temperate/boreal angiosperms). Thus, for effect parameter j, species sp, and biome–taxonomic group m, the model for $\mu_{\text{leaf},i}$ is:

$$\mu_{\text{leaf},i} = \log(k^{\star}_{\text{leaf},sp}) + \sum_{j=1}^{9} \alpha_{j,m} X_{j,i} + [\log(Q_{10}) + \alpha_{10,m} X_{9,i}] X_{10,i} \quad (1)$$

The main parameter of interest is $k^{\star}$ (i.e. $k^{\star}_{\text{wood}}$ and $k^{\star}_{\text{leaf}}$). It is standardized for the covariates (X) so that $k^{\star}$ represents the predicted k value when all covariates correspond to their mean (continuous covariates) or most commonly reported (categorical covariates) value across sites (definitions of X_1–X_{10} are provided in Appendix S3). We defined a hierarchical model for $k^{\star}_{\text{leaf},sp}$ that incorporates taxonomic relationships to facilitate estimates of data-poor species and improve convergence when faced with missing covariates (Ogle *et al.*, 2013). The hierarchical specification models species as nested in genus, genera nested in family, families nested in order and orders nested in major group. The model for wood $k^{\star}$ is similar, but differs in some of the methodological covariates; model details for both leaf litter and wood decomposability are given in Appendix S3, along with the prior distributions and the approach to imputing missing covariates. The HBMA models were implemented in OpenBUGS v.3.1.1 (Lunn *et al.*, 2009).

We combined the results from the wood and leaf decomposition models and evaluated the correlation between $k^{\star}_{\text{wood}}$ and $k^{\star}_{\text{leaf}}$ across 84 tree species represented in the overlap dataset to check for a global pattern of wood and leaf litter decomposability.

Global coordination of wood and leaf traits

Functional trait data were obtained from the global plant trait database TRY (Kattge *et al.*, 2011; Appendix S1). We focused on wood and leaf traits from living tissue that are: (1) important components of a potential WES or the LES, (2) potential drivers of wood and/or leaf litter decomposability, and (3) available for a sufficiently large number of species. These included: leaf nitrogen concentration (N_{leaf}), leaf phosphorus concentration (P_{leaf}), specific leaf area (SLA), leaf habit (evergreen versus deciduous), wood nitrogen concentration (N_{wood}), wood phosphorus concentration (P_{wood}), wood density (ρ_{wood}) and maximum tree height (h_{max}). Leaf habit was taken as a surrogate for leaf lifespan, which was not available for a sufficiently large number of species. Trait values were recorded as species means.

To test for a global convergence of wood and leaf traits, we used principal coordinate analysis (PCoA) based on a matrix of 1480 tree species representing all forest biomes (see Appendix S4 for the species list). Because data on N_{wood} and P_{wood} were only sparsely represented in the dataset, we conducted a second ordination with a subset of 149 species which included these two traits. The ordinations were based on a generalization of Gower's distance, which is suitable for the treatment of continu-
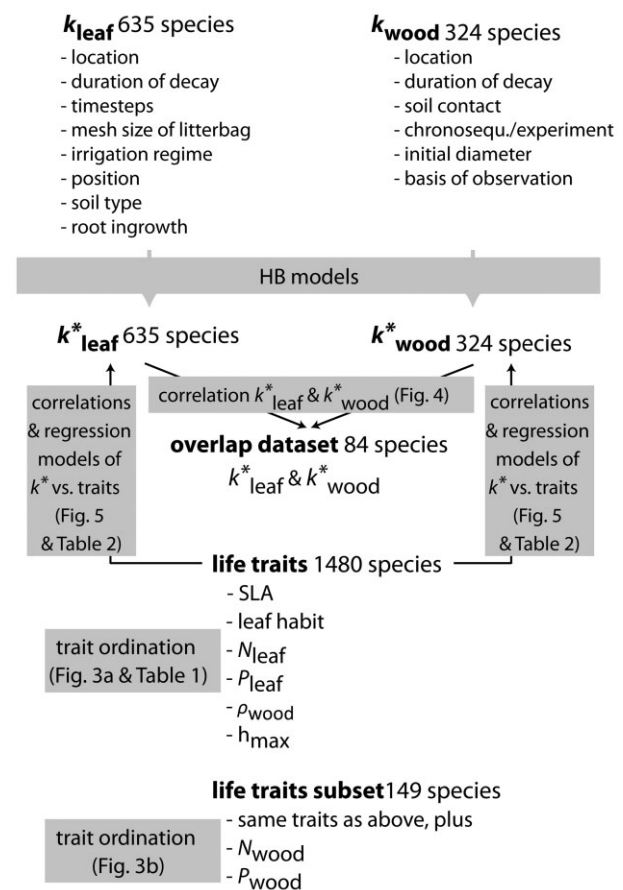

Figure 2 Representation of the data used in our study. The different datasets are indicated in bold; grey boxes show the analyses that have been conducted with these data and the respective figures and/or tables. The black arrows represent species-specific linkages of different datasets. k_{wood} and k_{leaf} represent the raw decomposition data with the associated metadata. $k^{\star}_{\text{wood}}$ and $k^{\star}_{\text{leaf}}$ represent the standardized decomposition rates which were obtained by hierarchical Bayesian (HB) modelling. The overlap data of decomposability rates comprise 84 species and represent species for which $k^{\star}_{\text{wood}}$ as well as $k^{\star}_{\text{leaf}}$ data were available. Life trait data for six traits were available from the TRY data base for 1480 species and a subset of these data, comprising 149 species, could be complemented with two wood chemical traits. The reference list of studies from which respective wood and leaf decomposition and trait data was obtained is given in Appendix S1. ρ_{wood}, wood density; h_{max}, maximum tree height; SLA, specific leaf area; N_{leaf}, leaf nitrogen content; P_{leaf}, leaf phosphorus content; leaf habit, deciduous versus evergreen; N_{wood}, wood nitrogen content; P_{wood}, wood phosphorus content.

ous and categorical variables and can accommodate missing data (Pavoine *et al.*, 2009). Figure 2 provides an overview of the trait and decomposition datasets used in this study.

Link between standardized decomposition rates and functional traits

We evaluated bivariate correlations among species-specific $k^{\star}$ ($k^{\star}_{\text{wood}}$ and $k^{\star}_{\text{leaf}}$) and five continuous functional traits (ρ_{wood},

Table 1 Functional traits included in the ordination of leaf and wood economics spectra and eigenvector scores of these traits along the first three PCoA axes.

	Trait	Range (mean)	% Missing data	PCoA 1	PCoA 2	PCoA 3
				32.40%	17.00%	12.50%
Angiosperms	SLA	1.10 – 43.2 (12.1)	–	0.927	−0.235	−0.291
and	N_{leaf}	5.60 – 48.0 (20.4)	–	0.632	−0.160	−0.759
gymnosperms	P_{leaf}	0.18 – 5.20 (1.24)	23.4	0.914	0.238	0.329
	Leaf habit	1, deciduous; 2, evergreen	2.6	−0.479	0.318	−0.818
	ρ_{wood}	0.28 – 1.15 (0.59)	–	−0.255	−0.955	−0.150
	h_{max}	0.10 – 67.10 (20.1)	41.6	−0.057	0.807	−0.588
				32.50%	16.80%	12.80%
Angiosperms	SLA	1.10 – 43.20 (12.4)	–	0.952	−0.224	−0.207
	N_{leaf}	6.50 – 48.0 (20.7)	–	0.611	−0.144	−0.779
	P_{leaf}	0.18 – 5.20 (1.24)	23.9	0.948	0.118	0.296
	Leaf habit	1, deciduous; 2, evergreen	2.7	−0.483	0.393	−0.783
	ρ_{wood}	0.28 – 1.15 (0.7)	–	−0.286	−0.939	−0.192
	h_{max}	0.10 – 60.0 (19.6)	42.9	0.016	0.464	−0.886
				45.00%	20.20%	11.90%
Gymnosperms	SLA	1.10 – 13.40 (6.6)	–	0.506	−0.333	−0.796
	N_{leaf}	5.60 – 22.60 (12.5)	–	0.891	−0.410	0.194
	P_{leaf}	0.21 – 1.96 (1.19)	10.5	0.866	0.441	0.236
	Leaf habit	1, deciduous; 2, evergreen	–	−0.588	0.574	−0.570
	ρ_{wood}	0.31 – 0.95 (0.51)	–	−0.359	−0.760	0.542
	h_{max}	0.44 – 67.1 (27.9)	8.8	0.336	0.718	0.610

SLA, specific leaf area (mm^2 mg^{-1}dw; dw, dry weight); N_{leaf}, leaf nitrogen content (mg g^{-1}dw); P_{leaf}, leaf phosphorus content (mg g^{-1}dw); ρ_{wood}, specific wood density (mg mm^{-3}); h_{max}, maximum tree height (m). PCoA1–3 represent the eigenvector scores of the six traits along the first three principal coordinate (PcoA) axes based on a matrix of 1480 species, and subsets of angiosperms (1423 species) and gymnosperms (57 species). Values in parentheses in the PCoA columns represent the variance accounted for by each axis.

h_{max}, SLA, N_{leaf}, P_{leaf}). Linear multiple regression models were used to evaluate k^* as a function of within-organ traits alone, and within- and cross-organ traits in concert. The trait values were z-transformed before entering multiple regressions to ease the interpretability of the results. Models of within-organ traits as covariates were compared with those of within- and cross-organ traits based on Akaike's information criterion (AIC). A lower AIC represents a better model fit.

All analyses were conducted in R 2.12 (R Development Core Team, 2012).

RESULTS

Global relationship of wood and leaf traits

Species-specific wood and leaf traits varied widely across species (*c.* 30–40-fold variation in P_{leaf} and SLA; nine-fold variation in N_{leaf}; four-fold variation in ρ_{wood}; Table 1). The ordination of six traits for 1480 species revealed significant relationships among wood traits and also among leaf traits. However, wood and leaf traits were clearly decoupled from each other (Fig. 3). Separate ordinations for angiosperms and gymnosperms revealed patterns within each group that were consistent with the combined analysis (Table 1, Appendix S5).

The first PCoA axis explained 32.4% of the total trait variation and was associated with LES traits (Table 1). This axis reflected a gradient from conservative leaf construction with low SLA, N_{leaf} and P_{leaf} (e.g. evergreen Pinaceae, Cupressaceae and Myrtaceae) to acquisitive leaf construction with high SLA, N_{leaf} and P_{leaf} (e.g. Betulaceae) (Fig. 3). The second PCoA axis explained 17.0% of the total trait variation and was primarily associated with wood traits (Table 1). This axis reflected a gradient from low h_{max} and high ρ_{wood} (e.g. Myrtaceae) to high h_{max} and low ρ_{wood} (e.g. Pinaceae and Cupressaceae). The third PCoA axis explained 12.5% of the total trait variation and was less clearly associated with either wood or LES traits (Table 1).

The PCoA on the subset of 149 species, including N_{wood} and P_{wood} data, revealed a similar result compared with the complete species dataset (Fig. 3b). Notably, variation in N_{wood} and P_{wood} aligned with the second PCoA axis in a way that high ρ_{wood} was associated with high N_{wood} and P_{wood}. Appendix S5 provides eigenvector scores of all eight traits along the first three PCoA axes and the associated variance explained by each axis.

The relationship between wood and leaf litter decomposability

The HBMA models fit the observed wood and leaf litter decomposition rates well (observed versus predicted R^2 = 0.95 and 0.80 for leaves and wood, respectively; Appendix S3). Moreover, most of the parameter estimates for the various covariate effects were highly significant and ecologically realistic (see Appendix S3 for
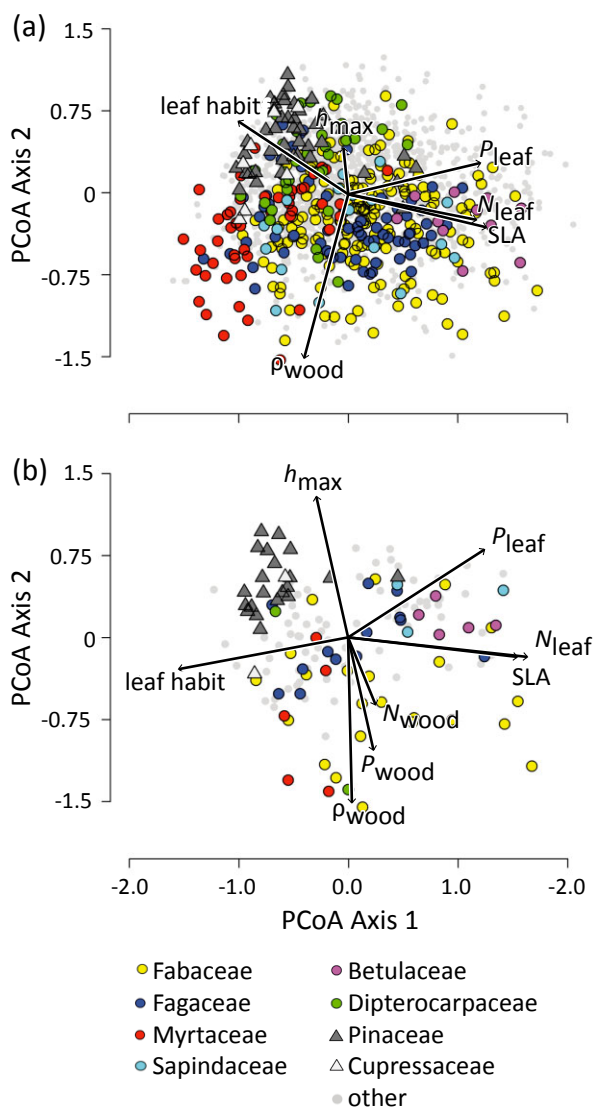
(a)

(b)

Figure 3 Principal coordinate analysis (PcoA) ordination of traits from living tissue illustrating decoupled trade-offs within wood traits and within the leaf economics spectrum of globally distributed tree species. (a) Ordination based on a matrix of 1480 species and six traits. The amount of explained variance of the axes and the eigenvector scores of all six traits along the first three PCoA axes are given in Table 1. (b) Ordination based on a subset of 149 species including two additional wood chemical traits. The amount of explained variance of the axes and the eigenvector scores along the first three PCoA axes are given in Appendix S5. Coloured symbols represent families for which decomposition data for wood and leaf litter for more than three species per family were available to this study. For trait abbreviations and data ranges see Table 1.

parameter estimates and a discussion of the model results). Standardized wood decomposition estimates ($k^\star_{wood}$) ranged from 0.026 to 0.178 year^{-1} across 324 species. Thus they were consistently lower than standardized leaf litter decomposition estimates ($k^\star_{leaf}$) ranging from 0.187 to 3.094 year^{-1} across
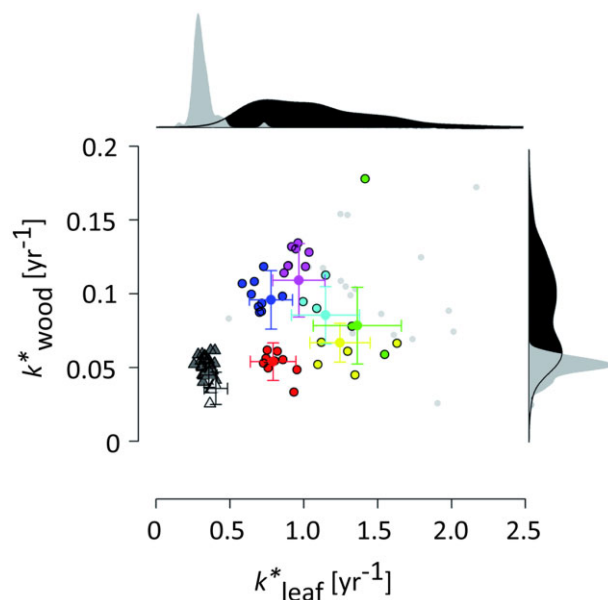

Figure 4 Relationship between $k^\star_{wood}$ and $k^\star_{leaf}$ across 84 tree species. Coloured symbols represent families for which more than three species per family were available in the subset of overlapping decomposability data. For colour-coding of the different families see legend to Fig. 3. Symbols with error bars represent family mean values considering all $k^\star_{wood}$ and $k^\star_{leaf}$ data ± SD (family-level results of the wood and leaf litter $k^\star$ models). The kernel densities correspond to the distribution of gymnosperms (grey) and angiosperms (black) for all $k^\star$ data on leaf litter for 635 species and on wood for 324 species.

635 species. Species-specific estimates of $k^\star$ are given in Appendix S6.

Estimates of both $k^\star_{wood}$ and $k^\star_{leaf}$ for the subset of 84 overlap species (56 angiosperms, 28 gymnosperms, including representatives of all major forested biomes) were a good representation of the data covered by all species (see kernel densities in Fig. 4). Across these 84 species, $k^\star_{wood}$ and $k^\star_{leaf}$ were positively correlated ($R^2 = 0.22, P < 0.001$; Fig. 4). This relationship, however, was only recovered across the combined dataset, with decomposition estimates consistently lower for wood and leaf litter of gymnosperms than angiosperms. The positive relationship of $k^\star_{wood}$ and $k^\star_{leaf}$ was not associated with variation in ρ_{wood} nor with LES traits across gymnosperms and angiosperms (Appendix S7).

$k^\star_{wood}$ and $k^\star_{leaf}$ were uncorrelated when evaluated separately for angiosperms or gymnosperms ($P = 0.56$ and $P = 0.15$, respectively), implying that the pattern found in the combined dataset was driven by the split between the two groups. These differences between the groups were most clear for leaves, such that $k^\star_{leaf}$ differed significantly between major groups. Generally gymnosperm leaves were more recalcitrant (low $k^\star_{leaf}$) than angiosperm leaves. No significant differences were evident between major groups for $k^\star_{wood}$, while species-specific $k^\star_{wood}$ and $k^\star_{leaf}$ values spanned a narrower range within the gymnosperms compared with the angiosperms (Fig. 4). For both groups, species-specific variation of $k^\star_{wood}$ and $k^\star_{leaf}$ was smaller within families than across different families (Fig. 4).
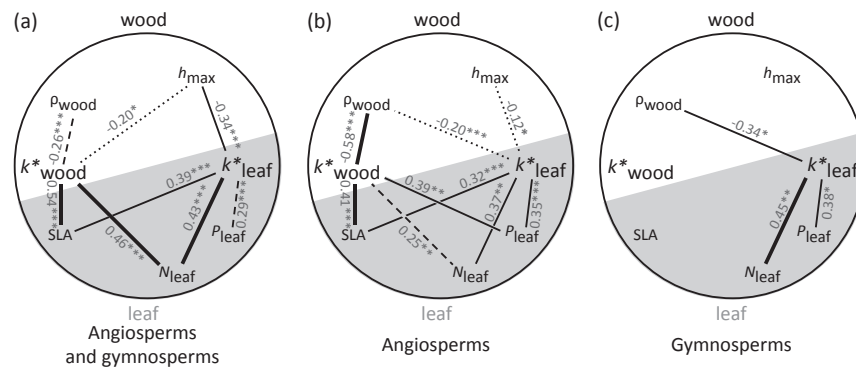
Figure 5 Pairwise correlations between continuous traits and k^*_{wood} or k^*_{leaf}, respectively. The two organs are distinguished by the colour of the spheres (leaf, grey; wood, white). Pearson's correlations for pairwise k^*-trait combinations of: (a) angiosperms and gymnosperms, (b) angiosperms only, and (c) gymnosperms only. The lines show significant correlations and their strength: dotted line, $r \leq 0.20$; dashed line, $r = 0.21–0.30$; thin solid line, $r = 0.31–0.40$; thick line, $r \geq 0.41$. Sample sizes vary between individual pairs (Appendix S8). For trait abbreviations see Table 1.

Decomposability–trait relationships within and between organs

Bivariate correlations of k^* and trait values were analysed together as well as separately for angiosperms and gymnosperms (Fig. 5). Across the two groups, ρ_{wood} and h_{max} were negatively correlated with k^*_{wood} ($r = -0.26$ and -0.20, respectively), and all three continuous leaf traits of the LES (SLA, N_{leaf}, P_{leaf}) were positively correlated with k^*_{leaf} ($r = 0.39$, 0.43, and 0.29, respectively; Fig. 5a). We further found that SLA and N_{leaf} exhibited a cross-organ correlation with k^*_{wood} ($r = 0.54$ and 0.46, respectively). Similarly, h_{max} was negatively correlated to k^*_{leaf} ($r = -0.34$). Within angiosperms, the correlation patterns were similar to those across angiosperms and gymnosperms, but the correlation of ρ_{wood} and k^*_{wood} was stronger ($r = -0.58$) while the one between h_{max} and k^*_{wood} disappeared (Fig. 5b). The correlations between all three leaf traits and k^*_{leaf} ($r = 0.32$, 0.37 and 0.35 for SLA, N_{leaf} and P_{leaf}, respectively) and the cross-organ correlations with the leaf traits and k^*_{wood} persisted ($r = 0.41$, 0.25 and 0.39 for SLA, N_{leaf} and P_{leaf}, respectively). Furthermore, k^*_{leaf} exhibited a negative relationship with ρ_{wood} ($r = -0.20$). Gymnosperms spanned a narrower range of k^* and trait values and included fewer species than angiosperms. They did not show any significant relationships between k^*_{wood} and the studied traits. k^*_{leaf} was positively correlated to N_{leaf} and P_{leaf} ($r = 0.45$ and 0.38, respectively) and negatively to ρ_{wood} ($r = -0.34$; Fig. 5c).

Cross-organ k^*-trait relationships were also evident in the multiple regression models for k^* of both organs. Models including both cross-organ and within-organ traits as predictors were always more parsimonious and explained a substantially higher amount of variation in k^*_{wood} as well as k^*_{leaf} than those including only within-organ traits (Table 2). Across all significant models the gain in explained variance by including cross-organ traits ranged from 3 to 49% with a mean of 18%.

DISCUSSION

We have presented a global comparative evaluation of species-specific wood and leaf decomposability (k^*) obtained by standardizing decomposition rates k for a wide range of environmental and study-specific variables. We demonstrate that functional traits of the LES and wood traits of a potential WES are good predictors of interspecific variation in leaf and wood k^*. This applies to relationships within and across organs. Our analysis further demonstrates that wood and leaf traits are not correlated globally, which reflects a decoupling of k^*_{wood} and k^*_{leaf} within angiosperms and gymnosperms. Among them k^*_{wood} and k^*_{leaf} were positively correlated, but this correlation could not be explained by generic trait differences. In addition, our analysis reveals strong phylogenetic patterns, as variation in species-specific k^* of both wood and leaves was much smaller within than across families.

Multivariate orthogonality of wood and leaf traits

It was expected that plants show a coordinated response across organs to gradients of environmental stress and disturbance (strategy theory; Grime, 1974; Westoby, 1998). This reflects the trade-off between rapid resource acquisition (e.g. light-demanding or pioneer species) and conservation of resources in well-protected tissues (e.g. shade-tolerant or climax species). However, our analysis of 1480 tree species from world-wide forest ecosystems does not support this idea; the primary axes of wood and leaf traits were close to orthogonal, suggesting independent underlying trade-offs between wood and leaf traits. This global pattern is similar to what has been described for trees of the tropical rain forest (Wright *et al.*, 2007; Baraloto *et al.*, 2010). Long-lived pioneers combine acquisitively constructed leaves for rapid growth and emergence to the canopy with conservatively constructed and durable wood for long-time persistence in the canopy (Loehle, 1988; Lusk, 1999). Such trees are

Table 2 Results from multiple regression models for k^*_{wood} and k^*_{leaf} as a function of within-organ, and within- and cross-organ traits.

	n	Within-organ traits			Within- & cross-organ traits		
		R^2	P	AIC	R^2	P	AIC
k^*_{wood}		$k^*_{wood} \sim \rho_{wood} + h_{max}$			$k^*_{wood} \sim \rho_{wood} + h_{max} + SLA + N_{leaf} + P_{leaf}$		
Angiosperms and gymnosperms	78	0.02	0.56	−532.98	**0.51**	< 0.001	−581.42
Angiosperms	57	**0.24**	< 0.001	−413.66	**0.38**	< 0.001	−419.06
Gymnosperms	21	0.11	0.36	−199.32	0.36	0.2	−200.25
k^*_{leaf}		$k^*_{leaf} \sim SLA + N_{leaf} + P_{leaf}$			$k^*_{leaf} \sim \rho_{wood} + h_{max} + SLA + N_{leaf} + P_{leaf}$		
Angiosperms and gymnosperms	181	**0.29**	< 0.001	−274.22	**0.43**	< 0.001	−309.12
Angiosperms	156	**0.17**	< 0.001	−243.43	**0.28**	< 0.001	−261.56
Gymnosperms	25	**0.58**	< 0.001	−121.92	**0.62**	< 0.01	−123.11

Within-organ traits for modelling k^*_{wood} were ρ_{wood} and h_{max}, and for k^*_{leaf} SLA, N_{leaf} and P_{leaf}. Models including within- and cross-organ traits incorporated all five traits.
For trait abbreviations see Table 1; AIC, Akaike's information criterion.
Significant models ($P < 0.05$) are indicated in bold; parameter estimates for all significant models are given in Appendix S9.

abundant in all forested climate zones and well known examples include some deciduous oaks as well as many tropical tree species.

Wood and leaf traits as predictors of wood and leaf litter decomposability

For angiosperms our results show that higher SLA, N_{leaf} and P_{leaf} lead to higher leaf decomposability. This suggests that resource allocation strategies and green leaf traits are closely linked to decomposability of the associated leaf litter. During senescence, retranslocation of nutrients from foliage to other plant parts may shift the nutrient concentration from fresh to senesced leaves. Thus the nitrogen and phosphorus concentrations of green leaves may not necessarily closely reflect the nutrient status of decomposing litter (Killingbeck, 1996). Yet our results showed important after-life effects of living tissue traits for litter decomposition, as previously reported at regional scales such as in a subarctic flora (Freschet et al., 2012), a tropical rain forest (Santiago, 2007) or a temperate grassland (Wardle et al., 1998). A direct link between traits of living and dead leaves may be especially pronounced for traits promoting structural or chemical protection, e.g. leaf tensile strength and secondary metabolite concentrations (Cornelissen et al., 1999; Hättenschwiler & Vitousek, 2000).

We showed a significant negative relationship between ρ_{wood} and k^*_{wood} in angiosperms, supporting the relationships between decay rates and wood mechanical strength (related to ρ_{wood}) from wood industry durability scores (Chave et al., 2009) and a local-scale Amazonian study (Chambers et al., 2000). For gymnosperms, none of the wood traits considered here were related to wood decomposability. This lack of correlation could reflect a true emergent pattern or alternatively it could be attributed to a smaller sample size, relatively narrow ranges of trait values and/or less variability in k^*_{wood} among gymnosperm species.

Decomposition is strongly mediated by the interplay between the decomposing substrate and the decomposer community (Dix & Webster, 1995). As a consequence, the relative importance of traits may vary with the perception of quality by different decomposers (Strickland et al., 2009). For certain species or intraspecific decomposition rates the stoichiometric demands of decomposers may be shifted in favour of elements other than N and P. Furthermore, the relative importance of certain traits such as N availability of the decomposing material may vary with the fertility of the surrounding soil and/or matrix litter. The magnitude of such discrepancies could not be tested with our data but is likely to contribute to the residual variation within the k^*-trait relationships.

A surprising result of our analysis was that the decomposabilities of wood and leaves are not only related to their 'own' tissue traits but also to those of the other organ. The emergence of cross-organ k^*-trait relationships in our analysis could be caused by commonly unmeasured traits relevant for decomposition. A link between k^*_{wood} and leaf traits could arise if leaf traits provide proxy information of an important wood trait that is lacking from the analysis. A likely candidate is the composition and concentration of secondary compounds impeding decomposition. Indeed, high SLA and N_{leaf}, indicative of acquisitive resource use with low investment in chemical protection, are positively correlated with k^*_{wood}.

Cross-organ k^*-trait relationships were consistently evident in our dataset within and across angiosperms and gymnosperms, indicating that such relationships will also occur at smaller spatial scales. This is backed up by evidence that more than half of the global variance in leaf traits occurs at local to regional scales (Wright et al., 2004; Freschet et al., 2011). Thus many contrasting plant economic strategies can be found within local species assemblages (e.g. Freschet et al., 2012).

We used the single negative exponential decay model (Olson, 1963) as a basis for calculating decomposability. This model assumes a constant relative decomposition rate through time. Yet long-term studies (e.g. Berg et al., 1993; Harmon et al., 2009) suggest that as decay proceeds the relative decomposition rate slows to a degree that cannot be captured by a single exponential

model. In other cases, an initial lag phase for colonization by decomposing organisms may occur during which decomposition proceeds slowly for a period of time, before increasing approximately exponentially (Freschet *et al.*, 2012). Despite these limitations we had to rely on *k*-values from single exponential models as these dominate the literature, and to address our hypotheses we needed to compile a large database with large taxonomic and global coverage. Using *k*-values introduces a bias when studies of different durations are pooled, because *k*-values tend to decrease with study duration (Berg & McClaugherty, 2008). We controlled for this by adding study duration as a covariate in the HBMA models and standardizing *k**-values for the mean durations separately for wood and leaf litter, and biomes and taxonomic groups (given in Appendix S3). The respective coefficients were negative (Figs S3.3 & S3.4 in Appendix S3), thus capturing the deceleration of the decomposition process over time. Consequently, we should be careful not to extrapolate *k* values based on our dataset for estimation of long-term decomposability or steady-state stocks.

Taxonomic pattern of decomposability

We expected wood and leaf decomposability to be decoupled, given that associated trade-offs within wood traits and within LES traits were independent of each other (Fig. 3). When decomposition rates were compared across all species, k^*_{wood} and k^*_{leaf} were weakly correlated (Fig. 4). However, this relationship could not be explained by generic differences in wood traits and/or LES traits between angiosperms and gymnosperms in accordance with organ-specific *k**-trait relationships. Wood density was generally higher in angiosperms (i.e. impeding decay) than in gymnosperms, but decay rates of gymnosperms were consistently lower than those of angiosperms. This also explains why the multiple regression between k^*_{wood} and wood traits alone (ρ_{wood} and h_{max}) was not significant across all species ($R^2 = 0.02$, $P = 0.56$, Table 2). Adding leaf traits positioned the gymnosperms at the very conservative end of the resource-use strategy spectrum and improved the model of k^*_{wood} significantly (Table 2). Corresponding to their conservative strategy, gymnosperms are well protected by large amounts of particularly recalcitrant forms of lignin and resins (e.g. Berg & McClaugherty, 2008). In addition, their low decay estimates compared with angiosperms might correspond to relatively lower N_{wood} and P_{wood} (Fig. 3b and Weedon *et al.*, 2009). In general, gymnosperms dominate nutrient-poor forests in harsh climates where they outperform angiosperms (Bond, 1989).

Within angiosperms and gymnosperms our results support the hypothesis that decoupling of wood and leaf traits is a component of decoupled decomposability (k^*_{wood} and k^*_{leaf}) of the two organs (Figs 1c & 4). However, cross-organ *k**-trait relationships may modify the proposed underlying mechanism. Variation in decomposability for both organs was lower within families than across them (Fig. 4). This is likely to relate to a high degree of host specificity of fungi that decay dead organic matter (Dix & Webster, 1995). Furthermore it suggests phylogenetic conservatism in traits related to decomposability, such that

species in the same family possess similar trait characteristics (Prinzing *et al.*, 2001). Clustering of species-specific *k** within genera or families might partly be driven by phylogenetic patterns observed for wood density. For 2456 Neotropical tree species, 74% of the species-specific variation in wood density is explained at the genus level (Chave *et al.*, 2006). There is also evidence that secondary chemicals, especially polyphenols and tannins, are phylogenetically conserved (Hegnauer & Hegnauer, 1964) and the effect of these compounds on decomposability can exceed that of tissue N or lignin content (Hättenschwiler & Vitousek, 2000). For example, stilbenes in *Eucalyptus* inhibit delignification of wood (Hart, 1981) which, in concert with high wood density, leads to low decomposability. Fagaceae are often well protected by large amounts of tannins inhibiting fungal growth. Protective substances in gymnosperms include terpenes, phenolic resins, flavonols, stilbenes and tropolones (Dix & Webster, 1995). To date, no conclusive generalizations about the relationships between secondary chemicals and decay rates can be made since only a few taxa have been studied.

With respect to the taxonomic patterning we cannot entirely exclude the possibility that modelling *k** with a taxonomic hierarchy pulls the estimates towards the genus and family means. The potential magnitude of this effect cannot be exactly quantified, as models without the taxonomic hierarchy show extremely poor convergence and yield highly uncertain *k** estimates for data-poor species. But it should be emphasized that we do not specify the degree of clustering (as defined by associated variance terms) within taxonomic groups a priori, but rather begin with the assumption that the variance terms are large (no clustering). The model fitting process uses the data to refine this prior assumption and indicates that such clustering agrees with the observed data.

CONCLUSIONS

Our analysis demonstrates that interspecific variation in the decomposability of wood and leaf litter – as well as trade-offs within wood traits and within the LES – are not coordinated among species within angiosperms and gymnosperms. Between these two major clades, decomposability of wood and leaf litter was positively related, but this relationship could not be explained by trait variation. Consistently lower *k** values for gymnosperms than angiosperms imply that a transition from gymnosperm to angiosperm forests, as predicted for the southern boundary of the boreal forest (Cramer *et al.*, 2001), may lead to faster nutrient and C cycling (but see Berg & Ekbohm, 1991). Our *k** approach can be seen as a simulated 'common garden' experiment of wood and leaf litter decomposition by means of statistical methods. A new generation of actual common garden experiments, where k^*_{wood} and k^*_{leaf} are quantified for a large number of tree species, will help to refine the results presented here. Two central findings, the strong phylogenetic signal in the k^*_{wood}–k^*_{leaf} space (Fig. 4) and the cross-organ *k**-trait correlations, suggest that the widely available decomposability predictors may not suffice to explain the emergent patterns, and that decomposition studies should include a characterization of

antimicrobial secondary compounds. The fact that SLA and N_{leaf}, two widely used model parameters for leaves which drive important physiological processes (Cramer *et al.*, 2001; Wright *et al.*, 2004; Bakker *et al.*, 2011), are not only good predictors for leaf decomposability but also for the decomposability of wood may further be exploited to improve predictions of nutrient and carbon cycling under future climate change and biodiversity scenarios.

REFERENCES

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.

Bakker, M.A., Carreño-Rocabado, G. & Poorter, L. (2011) Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Functional Ecology*, **25**, 473–483.

Baraloto, C., Paine, T.C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C. & Chave, J. (2010) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.

Berg, B. & Ekbohm, G. (1991) Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. *Canadian Journal of Botany*, **69**, 1449–1456.

Berg, B. & McClaugherty, C. (eds) (2008) *Plant litter. Decomposition, humus formation, carbon sequestration*. Springer, Berlin.

Berg, B., Berg, M., Bottner, P., Box, E., Breymeyer, A., Calvo de Anta, R., Couteaux, M., Escudero, A., Gallardo, A., Kratz, W., Madeira, M., Mälkönen, E., McClaugherty, C.,

Meentemeyer, V., Muñoz, F., Piussi, P., Remacle, J. & Virzo De Santo, A. (1993) Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.

Bond, W.J. (1989) The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society*, **36**, 227–249.

Brovkin, V., van Bodegom, P.M., Kleinen, T., Wirth, C., Cornwell, W., Cornelissen, J.H.C. & Kattge, J. (2012) Plant-driven variation in decomposition rates improves projections of global litter stock distribution. *Biogeosciences Discussions*, **8**, 8817–8844.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V. & Melack, J.M. (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.

Chapin, F.S., McFarland, J., David McGuire, A., Euskirchen, E.S., Ruess, R.W. & Kielland, K. (2009) The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences. *Journal of Ecology*, **97**, 840–850.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications*, **16**, 2356–2367.

Chave, J., Coomes, D.A., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Cornelissen, J.H.C., Pérez-Harguindeguy, N., Díaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F. & Cerabolini, B. (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist*, **143**, 191–200.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.

Dix, N.J. & Webster, J. (1995) *Fungal ecology*, 1st edn. Chapman and Hall, London.

Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P. & Aerts, R. (2010) Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, **98**, 362–373.

Freschet, G.T., Dias, A.T.C., Ackerly, D.D., Aerts, R., van Bodegom, P.M., Cornwell, W.K., Dong, M., Kurokawa, H., Liu, G., Onipchenko, V.G., Ordoñez, J.C., Peltzer, D.A., Richardson, S.J., Shidakov, I.I., Soudzilovskaia, N.A., Tao, J. & Cornelissen, J.H.C. (2011) Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography*, **20**, 755–765.

Freschet, G.T., Aerts, R. & Cornelissen, J.H.C. (2012) A plant economics spectrum of litter decomposability. *Functional Ecology*, **26**, 56–65.

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26–31.

Grime, J.P. (1979) *Plant strategies and vegetation processes*. Wiley, Chichester.

Harmon, M.E., Silver, W.L., Fasth, B., Chen, H., Burke, I.C., Parton, W.J., Hart, S.C. & Currie, W.S. (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Global Change Biology*, **15**, 1320–1338.

Hart, J.H. (1981) Role of phytostilbenes in decay and disease resistance. *Annual Review of Phytopathology*, **19**, 437–458.

Hättenschwiler, S. & Vitousek, P.M. (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology and Evolution*, **15**, 238–243.

Hegnauer, R. & Hegnauer, M. (1964) *Chemotaxonomy of plants, vol. 3 [Chemotaxonomie der Pflanzen, Band 3]*. Birkhäuser Verlag, Basel und Stuttgart.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Kattge, J., Díaz, S., Lavorel, S. *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Killingbeck, K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716–1727.

Loehle, C. (1988) Tree life-history strategies – the role of defenses. *Canadian Journal of Forest Research*, **18**, 209–222.

Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009) The BUGS project: evolution, critique and future directions. *Statistics in Medicine*, **28**, 3049–3067.

Lusk, C.H. (1999) Long-lived light-demanding emergents in southern temperate forests: the case of *Weinmannia trichosperma* (Cunoniaceae) in Chile. *Plant Ecology*, **140**, 111–115.

Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Moore, T.R., Trofymow, J.A., Taylor, B., Prescott, C., Camiré, C., Duschene, L., Fyles, J., Kozak, L., Kranabetter, M., Morrison, I., Siltanen, M., Smith, S., Titus, B., Visser, S., Wein, R. & Zoltai, S. (1999) Litter decomposition rates in Canadian forests. *Global Change Biology*, **5**, 75–82.

Niklas, K.J. (1992) *Plant biomechanics: an engineering approach to plant form and function*. University of Chicago Press, Chicago, IL.

Ogle, K., Barber, J. & Sartor, K. (2013) Feedback and modularization in a Bayesian meta–analysis of tree traits affecting forest dynamics. *Bayesian Analysis*, **8**, 133–168.

Olson, J.S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**, 322–331.

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S. & Daniel, H. (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, **118**, 391–402.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2383–2389.

Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. (2007) Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology*, **21**, 1016–1026.

R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, **94**, 13730–13734.

Santiago, L.S. (2007) Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology*, **88**, 1126–1131.

Strickland, M.S., Osburn, E., Lauber, C., Fierer, N. & Bradford, M.A. (2009) Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Functional Ecology*, **23**, 627–636.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, CA.

Wardle, D.A., Barker, G.M., Bonner, K.I. & Nicholson, K.S. (1998) Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology*, **86**, 405–420.

Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C. & Coomes, D.A. (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters*, **12**, 45–56.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.

Wirth, C. & Lichstein, J. (2009) The imprint of species turnover on old-growth forest carbon balances – insights from a trait-based model of forest dynamics. *Old-growth forests*, pp. 81–113. Ecological Studies 207. Springer, Berlin.

Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A., Poorter, L., Silman, M.R., Vriesendorp, C.F., Webb, C.O., Westoby, M. & Wright, S.J. (2007) Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany*, **99**, 1003–1015.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Bibliographic reference of studies from which data was used for this analysis.

Appendix S2 Study locations for wood and leaf litter decomposition.

Appendix S3 Model description for standardization of wood and leaf litter decomposition rates and discussion of model results.

Appendix S4 List of 1480 species included in multivariate trait analyses.

Appendix S5 Additional results of the multivariate trait analyses and bivariate trait correlations.

Appendix S6 Posterior k^* estimates for wood and leaf litter of all species with available k data.

Appendix S7 Species-specific correlations between ρ_{wood} or the leaf economics spectrum, and k^*_{wood} or k^*_{leaf}, respectively.

Appendix S8 Correlation coefficients, P-values and degrees of freedom for pairwise k^*-trait combinations.

Appendix S9 Parameter estimates of multiple regressions for k^*_{wood} and k^*_{leaf} as a function of traits.

BIOSKETCH

The working group initiated by **C. Wirth** and **J. H. C. Cornelissen** and funded by ARC-NZ Network for Vegetation Function (WG 35) met in Akaroa, New Zealand, to synthesize global datasets on plant traits and wood and leaf litter decomposition. It brought together experts on trait-based plant ecology (**W. K. Cornwell**, **J. H. C. Cornelissen**, **J. T. Weedon**, **I.J. Wright**, **A. E. Zanne**), biogeochemistry and forest ecology (**B. G. Jackson**, **D. A. Peltzer**, **D. A. Wardle**, **C. Wirth**), ecoinformatics (**G. Boenisch**, **J. Kattge**) and Bayesian statistics (**K. Ogle**). **J. M. Craine**, **J. P. Penuelas** and **P. B. Reich** provided data and contributed to the writing of the manuscript. **K. A. Pietsch** is a PhD student in the Wirth lab and she has led the study. Her research focuses on deadwood dynamics and the role of tree diversity on wood decomposition.

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