The leaf economic spectrum drives litter decomposition within regional floras worldwide

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Leaves are the green machines that drive terrestrial oxygen production, carbon assimilation and primary productivity worldwide. Some green machines are fast but short-lived producers, while others are durable enough for steady carbon gain over the long term. The nuts and bolts of the green machinery to support fast production versus durability are the chemical, physiological, and structural traits of the plant species that together shape the globally operating “leaf economics spectrum”. These green-leaf traits have crucial implications not only for the production of biomass in biogeochemical cycles, but also for its subsequent fate: the litter traits inherited from the green leaves together with the litter environment drive the rate of litter decomposition. From a global synthesis of 818 species in 66 decomposition experiments on six continents, we quantified the degree to which functional differentiation among species affects their litter decomposition rates. For the first time at global scale, we show that: (1) the magnitude of species-driven differences in decomposition within biomes is larger on average than climate-driven variation across biomes; (2) the decomposability of a species’ litter is consistently correlated with that species’ position on the green-leaf economics spectrum: species designed to achieve a fast return on carbon invested in leaves produce faster decomposing litter compared to those species with a slower-return strategy. These results suggest that a shift in relative abundance of particular species traits within a biome could strongly impact overall decomposition rates. Correctly predicting the abundance and distribution of particular plant traits will be crucial for accurate forecasts of future carbon pools and their feedbacks to further climate change.

Litter decomposition in terrestrial ecosystems has a profound effect on global carbon cycles, affecting atmospheric CO₂ and climate through litter carbon respiration and via accumulated litter as fuel for wildfires. The multiple drivers of decomposition include climate, species litter quality, and decomposition micro-environment.
Climate sets broadly similar conditions for long-term litter decomposition within biomes. In contrast, interspecific differences in green leaf characteristics and litter characteristics are associated with different plant strategies within biomes. These characteristics are modulated only modestly by climate, and over 40% of global variation for particular leaf traits can be found within individual sites. The pronounced within-site variation among species can be due to finer-scale environmental heterogeneity in space (e.g. soil fertility and hydrology) and time (e.g. disturbance) affecting within-site trait differentiation. We therefore hypothesized that variation in leaf litter decomposition rates within climate regions worldwide would be a function of the traits of plant species.

We brought together data from published and unpublished experiments (Assembly of Research on Traits and DEComposition: ART-DECO project). Our focus was on datasets from experiments that incubated leaf litter of many species in a common environment, holding climate, soil environment, decomposer community, and incubation period constant within each study. In total, the database contains 1196 records of species-by-site combinations from 66 sites including 818 species from 165 plant families. The sampled diversity largely parallels the mix of diversity among higher plant taxa: the dataset includes 580 eudicot species, 118 monocots, 22 species from the Magnoliid lineage, 39 Gymnosperms, 37 Pteridophytes (ferns and fern allies), and 20 Bryophytes. The broad coverage of our dataset and advanced meta-analytic methods allowed us to isolate species-specific decomposability within each study, and to search for decomposition relationships with continuous traits, plant functional types, and phylogenetic groups that are consistent across studies.

How wide is the variation in leaf decomposition rates due to species traits, compared to climate-driven variation? To calculate the magnitude of the species-based effect while holding climate constant, we considered only studies that sampled > 20 species from
one climatic zone, leaving 14 studies. On average, these studies found an 18.4-fold range in decomposition rate. Considering only the middle 90% of the species in each study (between the 5th and 95th quantile), there was a 10.5-fold average difference in species decomposition rates (size of circles in Figure 1). Further, large variation in litter decomposition rates was observed among species in all climate zones from the arctic to the tropics (see distribution of circles, Fig. 1), demonstrating that a wide range of decomposition rates among species is a common feature of natural ecosystems.

We compare these results to those of two large-scale experiments decomposing the same litter in very different climate conditions. In North America Parton et al. found a 5.5-fold range in decomposition rate of a common substrate, with the fastest decomposition in a wet tropical forest and the slowest in the tundra. In another large study spanning sites in Europe and North America Berg et al. found a 5.9-fold range in the rate of decomposition for pine litter across sites.

What underlies the large differences in species decomposition rates? Plant species range from those that obtain a strategically slow return on carbon invested, often coupled with efficient nutrient use and/or extended durability, as indicated by high leaf mass per area (LMA) or low mass-based leaf nitrogen concentration ($N_{\text{mass}}$), to those capable of gaining a fast return on leaf carbon associated with the opposite traits. These green leaf traits are tightly correlated with the chemistry of senesced leaves ($r=0.76$ for green leaf and litter N in this dataset). Here we show, for the first time at a global scale, that these leaf “economic” traits lead influential afterlives. Green-leaf traits drive decomposition rates within sites across biomes because the same characteristics that influence the physiology and protective features of the green leaves also affect the activity and abundances of the detritivores.
For each study we quantified the relationship between decomposition rate and leaf traits (both of green leaves and of litter). Both green leaf and litter traits were correlated with decomposition with roughly equal variance in decomposition explained by each green leaf or litter trait (Fig. 2). There was also significant colinearity among predictors: litter % N was positively correlated with litter %P ($r=0.50$, $P<0.001$), and negatively correlated with LMA ($r=-0.45$, $P<0.001$), but uncorrelated with litter lignin ($r=0.01$, NS). Thus, positive effects of other nutrients and/or negative effects of thicker leaves on decomposition may contribute to the positive relationship between decomposition and leaf and litter %N. Furthermore, since litter N and lignin were unrelated, both carbon chemistry (i.e., lignin) as well as traits associated with the green leaf economics spectrum appear important in influencing decomposition.

We found consistent large differences in decomposability among vascular functional groups (Figure 3). Woody deciduous species—generally faster-return plants with shorter individual leaf lives than woody evergreens—produced litter that decomposed 60% faster than woody evergreen species. This was true whether the evergreen species included both gymnosperms and angiosperms or only the latter. Surprisingly, herbaceous species did not produce litter that decomposed faster than woody species. This was due to slow decomposition among graminoids (grasses and grass-like monocots), which balanced fast decomposition among forbs (eudicot herbs). These differences in decomposition are consistent with differences in mean green leaf %N among angiosperm graminoids, forbs, shrubs and trees, when comparing species with comparable tissue longevities. In contrast to the large differences between forbs and graminoids, species that have the capacity to fix atmospheric N produced litter that decomposed only slightly (and non-significantly) faster than non-N fixers.

Decomposability of litter also differs systematically among the large clades within the higher plant phylogeny (Figure 3a). Eudicot litter decomposed faster than four out
of five more basal clades both across all species and within specific growth forms. Global mean effect sizes demonstrate that eudicot litter decomposed on average four times faster than bryophyte litter, three times faster than litter of ferns and their allies, 1.8 times faster than gymnosperm litter and 1.6 times faster than monocot litter. One of the key uncertainties in forecasts of the carbon cycle are potential shifts in the identity and traits of the dominant plant species, which have feedbacks to the climate cycle through numerous mechanisms including decomposition rate. The magnitude of the differences reported here suggests that shifts in the relative abundance of these already co-existing groups (e.g., a decrease in the abundance of slow decomposing bryophytes in the tundra) in response to climate change could have large effects on regional soil carbon cycles.

In summary, the traits of green leaves of different species vary widely within particular biomes down to the plot scale. This variation is associated with different “economic” strategies for carbon gain and growth and with different phylogenetic groups. This functional differentiation has large and consistent afterlife effects on the rate of decomposition of senesced leaves, an effect that on average is much larger than the effect of climate on decomposition. These results demonstrate that correctly predicting the abundance and distribution of particular species traits and their associated decomposability under future climates is crucial for accurate forecasts of future carbon cycling rates and ecosystem feedbacks to the climate system.

Methods

Species-specific decomposition records and the traits of leaves and undecomposed leaf litter were collected from published and unpublished sources based on experimental multi-species incubations (see appendix). In most cases, the data were contributed directly by the lead author of the original experiment, allowing the original researcher to
classify species functional traits and to include unpublished values for particular traits. In experimental studies only the control groups were used. Species decomposition records were collected as percent mass loss for each successive harvest, and decomposition constants \((k)\) were calculated for each species-experiment combination.\(^{21}\)

Standard meta-analysis techniques (MetaWin v2.0) were used to quantify the degree of congruence among results from studies undertaken under a variety of climatic and experimental conditions. Response ratios were used to compare effect sizes from the set of studies, with study included in the model as a random factor. Uncertainty surrounding estimates of effect size were described using (non-parametric) bootstrap confidence intervals. For pairwise comparisons of group-mean effect size (e.g., deciduous vs evergreen woody species), only studies with \(>2\) species were included in each group. Mean slope estimates and statistical significance of trait-decomposition relationships were derived from mixed-effects ANCOVA, with study treated as a random factor and traits used sequentially as covariates. We also calculated weighted estimates of regression coefficients for the trait-decomposition relationships.\(^{22}\)

‘Supplementary Information accompanies the paper’

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**Figure 1.** The magnitude of the species effect on decomposition within regional floras located in widely varying climate conditions across the world. Each cross in the figure and dot on the map represents a multi-species decomposition study at the modelled long-term climate.\(^{23}\) For 14 large sample size (\(>20\) species) studies we calculated the change in decomposition rate for the middle
90% of species (from the 5th to the 95th quantile). We then represent the proportional difference within each study as the diameter of the circles (arbitrary scale). This species-based effect (holding climate constant within each study) can be compared to published measures of the range of decomposition rates observed due solely to climate-based variation (holding species constant). Two large across-climate studies of the same litter found 5.5 and 5.9 fold ranges in decomposition rates among different biomes. On average, species-based effects were substantially larger than climate-driven effects, showing an 18.4-fold mean difference when all data were considered, and 10.5-fold mean difference when only the central 90% of species were included in the analyses.

**Figure 2.** Meta-analysis of the relationships between green leaf or leaf litter traits and decomposition rate \((k)\) within studies across the world. All comparisons are within studies with climate and experimental methods held constant. The number of studies that measured each trait varies and is reported in panel A. Panel A shows the log-log scaling slope for each trait. Panel B shows the sample size weighted mean correlation coefficient. Water and acid soluble polysaccharide fraction consists largely but not exclusively of cellulose and hemicellulose. Associated ANCOVAs found each of the six traits significant at \(P<0.01\).

**Figure 3.** Effect size estimates from meta-analysis for pairwise phylogenetic and functional group comparisons, including studies that had a minimum of two species in each group. All comparisons are within studies with climate and experimental methods held constant. In panel A the decomposition of bryophytes, ferns and fern allies, gymnosperms and Magnoliids are compared to the eudicots. In panel B we make pairwise comparisons between woody and herbaceous species, evergreen woody and deciduous woody species,
herbaceous forbs and herbaceous graminoids, and species with and without the ability to fix atmospheric N. Error bars represent the 95 % confidence intervals obtained through bootstrapping. Please note the shift in the y-axis scale between panel A and B.

Diameter = range of decomposition rate for the same litter in widely varying climates

Multi-species decomposition experiment

Circle diameter represents the range in decomposition rate for the middle 90% of species in each study of >20 species


Diameter = range of decomposition rate for the same litter in widely varying climates
25 studies
Water and acid soluble polysaccharides
18 studies
Lignin
42 studies
LMA
22 studies
Green leaf “economic” traits

Scaling slope +/- SE
Faster decom.
Slower decom.

Correlation coefficient +/- 95% CI

(A)

N 25 studies
Litter traits
N 59 studies
P 48 studies
Lignin 42 studies
Water and acid soluble polysaccharides 18 studies

(B)

N
Green leaf “economic” traits

N
Litter traits
P

Lignin
Water and acid soluble polysaccharides

LMA
Mean effect size +/- 95% CI

- Eudicot decomposition rate (control)
- Magnoliids
- Bryophytes
- Gynosperms
- Monocots
- Ferns and fern allies
- N=5 studies
- N=6 studies
- N=16 studies
- N=25 studies
- N=6 studies

- Faster decompos.
- Slower decompos.

- Evergreen
- Woody
- Deciduous
- Forbs
- Herbaceous
- Graminoids
- Non N-fixers
- N-fixers
- N = 20 studies
- N = 19 studies
- N = 21 studies
- N = 12 studies

- Slower decompos.
- Faster decompos.

- within woody species
- within herbaceous species
The ART-Deco database includes data from these published papers:


