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Abstract

Strong relationships exist between litter chemistry traits and rates of litter decomposition. However, leaf traits are more commonly found in online trait databases than litter traits and fewer studies have examined how well leaf traits predict litter decomposition rates. Furthermore, while bulk leaf nitrogen (N) content is known to regulate litter decomposition, few studies have explored the importance of N biochemistry fractions, such as protein and amino acid concentration. Here, we decomposed green leaves and naturally senesced leaf litter of nine species representing a wide range of leaf functional traits. We evaluated the ability of traits associated with leaf and litter physiology, N biochemistry, and carbon quality to predict litter decomposition. The objectives of this study were to determine if 1) N fractions explain variation in decomposition that is not explained by bulk N parameters alone, and 2) green leaf traits, as opposed to litter traits, can accurately determine rates of litter decomposition. We found N biochemistry traits to have similar predictive power to that of bulk N. We also found that leaf N biochemistry traits correlated strongly with each other and aligned on a single axis of variation resembling that of the 'leaf economic spectrum.' We noted that green leaf traits associated with this axis, including bulk N, N fractions, leaf mass per area, and lignin, were better predictors of decomposition than litter traits and concluded that leaf trait databases may be used to accurately predict litter decomposition. Future decomposition studies should consider fitting the more flexible Weibull distribution model to litter cohorts, as this model is much less rigid than the classic exponential decay model traditionally used in decomposition studies.

Keywords: leaf economics spectrum; Lignin; plant functional traits; leaf nitrogen; litter decomposition; decomposition

Introduction

Litter decomposition plays a major role in nutrient cycling in most terrestrial ecosystems of the world (Aerts, 1997; Meentemeyer, 1978; Swift & Anderson, 1989) and is responsible for up to 70% of the total annual C release from soils, estimated at 68 Pg C yr^{-1} (Raich & Schlesinger, 1992). At the global scale, rates of decomposition are thought to be primarily controlled by climate (e.g., temperature and precipitation), with litter quality and decomposing organisms playing important yet comparably minor roles (Dyer, Meentemeyer, & Berg, 1990; Meentemeyer, 1978). However, new evidence suggests that this assumption is the result of aggregating regional-scale variation into mean values in Earth-system models (Bonan et al. 2013), and that decomposer communities and litter quality play a more direct role in determining decomposition rates (Bradford et al. 2016). Thus, recent work has focused on the role of litter quality and decomposer communities on decomposition at broad scales (e.g. Zhang et al. 2008, Strickland et al. 2009, Pietsch et al. 2014, Bradford et al. 2016).

Litter quality is often characterized by lignin concentration (Meentemeyer 1978, Aerts 1997), the ratio of lignin to N (Scott and Binkley 1997, Zhang et al. 2008), and the ratio of C to N (Berg & Ekbohm, 1991). Lignin is one of the slowest decomposing components of plant litter. High initial lignin concentrations can increase the amount of immobilized N per unit C in litter (Melillo et al. 1982), resulting in a strong relationship between decomposition rate and initial lignin:N (Berg & Staaf, 1980; Melillo et al., 1982; Rahman, Tsukamoto, Yoneyama, & Mostafa, 2013). Phenolics, aromatic compounds produced to protect plants against environmental stressors, can slow rates of decomposition. Previous studies suggest decomposers prefer more labile litter

compounds, such as carbohydrates, to phenolics in litter (Rovira and Vallejo 2002). Studies have also used bulk leaf N content (LNC) as a metric to study leaf litter decomposition (Bakker et al. 2011). While bulk LNC is known to regulate litter decomposition, few studies have explored the importance of N biochemistry fractions. In many species, the vast majority (~85%) of leaf nitrogen is allocated to nucleic acid, amino acid, and protein content, all of which are highly labile (Funk et al. 2013). However, other fractions such as N-based secondary compounds and cell wall protein may be comparably recalcitrant or inaccessible, resulting in slower decomposition.

Green leaves (here, recently matured, sun leaves) and freshly senesced leaf litter have important differences in chemical composition. For example, a meta-analysis by Aerts (1996) showed that approximately half of the bulk N and P concentrations in mature leaves of perennial shrubs were resorbed prior to senescence across studied species. The resulting litter will have a higher concentration of lignin and other recalcitrant C components compared to green leaves. Because litter traits more accurately reflect the leaf chemistry of naturally senesced litter, it may be expected that these traits would be better predictors of litter decomposition. However, determining green leaf traits that can accurately predict rates of decomposition can be useful, for where green leaf trait databases are extensive within the literature (e.g. TRY, Kattge et al. 2011), less information is available for litter traits.

Here, we determine the relative ability of leaf and litter traits to predict litter decomposition. The first objective of this investigation was to determine if N fractions may improve efforts to accurately predict rates of decomposition. Our second objective was to determine if green leaf traits, as opposed to litter traits, can accurately determine rates of litter decomposition. We examined litter

decomposition in nine species with a large range of biochemical and physiological traits. In addition to standard physiological traits (e.g., leaf mass area, photosynthetic rate) and C quality components (e.g., lignin, phenolics), we measured N allocation into five biochemical pools: nucleic acid, amino acid, soluble protein (includes Rubisco), thylakoid protein, and cell wall protein. As the importance of litter-environment interactions is well documented in the literature, we decomposed leaves in two contrasting southern California plant communities: a coastal sage scrub (CSS) community and a riparian oak (RO) community. These sites were chosen based on observed differences in soil temperature and moisture; CSS is generally warmer and drier, where RO is comparatively cooler and more humid.

Materials and methods

Functional trait measurements

We selected nine species with a broad range of biochemical and physiological traits (Table 1, Table S2). Plants were located on the campus of Chapman University (33° 47'37''N, 117° 51'00''W) or California State University, Fullerton (33° 52'58''N, 117° 53'13''W). All leaf measurements were conducted in May 2010 on a recently-matured, sunlit leaf from five individual plants of each species. Photosynthetic rate, transpiration rate, and chlorophyll fluorescence were measured with a LI-6400 portable gas exchange system (LI-COR, Lincoln, NE, USA). Measurements were conducted at 400 µL L^{-1} CO_2 and 2000 µmol photon m^{-2} s^{-1}. Leaf temperature was kept constant at 25°C and relative humidity varied between 45-60%. Water use efficiency (WUE) was calculated as the ratio of photosynthesis to transpiration. The effective quantum yield of PSII (ΦPSII) was calculated as $(F_m'-F_s)/F_m'$, where F_s is the fluorescence yield

of a light-adapted leaf and F_m' is the maximal fluorescence during a saturating light flash. We used a SPAD-502 meter (Spectrum Technologies, Plainfiled, IL, U.S.A.) to estimate chlorophyll content, as SPAD values are highly correlated with leaf chlorophyll concentrations.

After physiological measurements, live green leaves (i.e. young, fully matured leaves exposed to full sun) and freshly fallen, senesced leaves (i.e., litter) were harvested from five individuals per species, scanned for leaf area, and dried at 60^{o}C to calculate leaf mass area (LMA). Leaves and litter were then ground to pass a 40-mesh (420 µm) screen and analyzed for leaf N with an elemental analyzer (Costech 4010 elemental combustion system, Pioltello, Italy), total phenolics using a Folin-Ciocalteu assay (AOAC 1950), and lignin using an acid detergent extraction at the UC Davis Analytical Laboratory. Samples from multiple leaves were combined for LMA and lignin analysis.

We analyzed protein fractions, nucleic acids, and amino acids using a second set of green leaves and litter (complete methodology developed and included in Funk et al. 2013). Briefly, water-soluble, SDS-soluble, and SDS-insoluble protein fractions were extracted using a modified version of Takashima, Hikosaka, & Hirose (2004) where the soluble fraction consists primarily of Rubisco (Terashima and Evans 1988), the SDS-soluble fraction consists of membrane-bound proteins, and the SDS-insoluble fraction consists of cell wall proteins. Nucleic acids were extracted with chloroform and methanol using a modified version of Chapin & Kedrowski (1983). The supernatant containing total nucleic acid was digested using a persulfate digest method (Bronk, Lomas, Glibert, Schukert, & Sanderson, 2000). Amino acids were extracted using a modified version of Noctor et al. (2002) using 80% methanol

(Noctor et al. 2007) and quantified using a modified version of the ninhydrin method (Sun et al. 2006) for use with a microplate reader.

Litter decomposition experiment

Freshly fallen, senesced leaves from the same group used for chemical analysis were air dried at 25^{o}C for one week and placed in litterbags. Litter bags were approximately 10 cm^2 and constructed using 1 mm mesh fiberglass screen and staples (Funk 2005). Bags were filled with 1 g of dried litter, which was cut into pieces in order to fit in the litterbags. Due to limited leaf material, only 0.5 g of *Ficus benjamina* and *Alocasia odora* litter were used. In total, 540 bags were constructed: 2 sites x 9 species at each site x 6 collection dates (see below) x 5 replicates.

Once filled, bags were deployed in the field in December 2009. Two sites were chosen within Irvine Regional Park in Orange, CA: an open site consisting of coastal sage scrub (CSS) vegetation (33^{o} 48.346' N, 117 ^{o} 45.407' W) and a shaded, riparian oak woodland (RO) (33 ^{o} 48.477' N, 117 ^{o} 45.351' W). At the CSS site the bags were placed on the soil surface which contained very little litter at the time of deployment. The bags in the RO site were deployed on the surface of the standing litter layer. Within each site, bags were strung together in five groups, with each group containing a bag of each species. Litter bags were retrieved 0.1, 0.3, 0.5, 0.8, 1.0, and 1.5 years after the December deployment date. After collection, litter bags were air dried for one week and weighed to determine mass loss.

On each collection date, air temperature was measured 0.5 m above each litterbag group. Soil temperature was measured at a depth of 5 cm using a digital thermometer (Hanna Instruments). Three cores of soil were collected using a turf auger to a depth of ~10 cm for each replicate set of litter bags.

Within 24 hours of collection, vegetation and rocks were removed from the soil by hand. A subsample was dried at 105 ^{0} C for 48 hours to calculate gravimetric water content (GWC). An additional 12 g of field-moist soil was extracted with 50 mL of 2M KCl by shaking at 200 rpm for 24 hours. The extract was filtered through GFF filters and frozen until analysis for NH_4^+ and NO_3^- using colorimetric methods adapted for 96-well microplates (Allison, McGuire, & Treseder, 2010). Soil organic matter was measured as loss of ignition at 550 °C.

Statistical analysis

We fit the proportion of mass loss for each species-site combination to a Weibull residence model:

$$F(t, \alpha, \beta) = e^{-(\frac{t}{\beta})^{\alpha}}$$

where β represents the "scale" parameter and α represents the "shape" parameter (*see* Cornwell and Weedon 2014). If α = 1, β becomes equivalent to the inverse of *k* in the exponential decay model. We used an optimization algorithm for fitting both α and β parameters in accordance with supplementary information of Cornwell and Weedon (2014). Weibull residence models for each species-site combination provided better performance than the classic exponential decay model (lowest Akaike information criteria, Akaike 1998).

All analyses were conducted in R (R3.3.3, R Core Team, 2017). Leaf and litter trait data that violated assumptions of homogeneity of variances and normality were log transformed. All data that was log transformed met statistical assumptions post-transformation.

A principal component analysis (PCA) was used to identify trade-offs among traits (psych package). Because of the large number of traits and relatively small number of species, we eliminated redundant traits (traits that

were strongly correlated with several traits) from our PCA analysis (Table 2, Figure S1). For the leaf trait PCA, we eliminated lignin:N, C:N, ΦPSII, soluble protein, membrane protein, cell wall protein, and nucleic acid. For the litter PCA, we eliminated lignin:N, soluble protein, membrane protein, cell wall protein, and nucleic acid. Thus, carbon quality was represented by lignin and phenolics while nitrogen quality was represented by bulk N, total protein, and amino acid concentration. Analyses were conducted on standardized species means. Axes were constrained to the first four components to improve axis interpretability. We used a multiple regression to fit predicted decomposition values from the Weibull residence models to principal component loadings in order to determine traits that best predicted decomposition.

Differences in decomposition rate at each time point are included in the supplementary information. We used a two-way ANOVA with species and site as the main effects on mass loss (agricolae package; de Mendiburu 2017). We used unpaired student's t-tests to determine differences in environmental conditions between the CSS and RO sites.

Results

Species-based decomposition curves varied greatly in mass loss, with the fastest decomposition rates observed in *Alocasia odora,* followed by two N-fixing species (*Erythrina* sp. and *Gleditsia triacanthos*) and *Gingko biloba* (Figure 1, Figure S2). Differences in mass loss varied less by site than by species, with significant site effects only reported at 0.8 and 1 years (Table S1). We did not report species-site interactions over the course of this experiment.

Leaf and litter traits

Leaf and litter traits varied greatly across our nine species with 4-fold differences in LMA and N concentration, and 10-fold differences in lignin and N

biochemistry traits (Table S2). Many traits showed strong correlations with one another (Figure 2). For example, N biochemistry (protein fractions, amino acid and nucleic acid concentration) and carbon quality (lignin, C:N) traits were negatively correlated with each other in both leaves and litter.

Four PCA axes captured the majority of the variation across species average *leaf* traits (92% of total variation with varimax-rotated PCA; Figure S1, Table 2). The first axis (47% of variation) captured a trade-off between N biochemistry (high protein, amino acid, and bulk N concentration) and structure (high LMA, lignin). The second axis (18% of variation) was associated with species variation in carbon assimilation. The third and fourth axes (14 and 13% of variation) captured variation in phenolics and chlorophyll concentration, respectively.

Four PCA axes also captured a large portion of variation across species average *litter* traits (91% of total variation; Figure S1, Table 2). The first axis (35% of variation) captured a trade-off between bulk N concentration and phenolics. The second axis (23% of variation) captured variation in N biochemistry (total protein and amino acid concentration). Note that these two N biochemistry fractions were decoupled from bulk N for litter. The third and fourth axes (18 and 15% of variation) captured variation in LMA and lignin concentration, respectively.

Decomposition patterns and predictors

Green leaf traits associated with variation in PC1 and PC2, and litter traits associated with PC1 and PC4 were powerful predictors of decomposition rate (Table 3). Thus, *leaf* traits associated with N biochemistry, structural components, and carbon assimilation were significant predictors of decomposition. Further, *litter* bulk N concentration, phenolics, and lignin were

found to be powerful predictors decomposition rate. None of the litter N biochemistry parameters included in this study predicted decomposition rate. Collectively, litter from species with higher leaf N quality and carbon assimilation rates decomposed faster, while litter from species with higher investments in structure (LMA, lignin) decomposed more slowly. LMA, a trait that has been shown to predict decomposition in other systems, was correlated with decomposition as a leaf trait but not as a litter trait (Table 2, 3).

Differences between sites

The CSS community displayed higher soil temperature, and lower organic matter, total N, and GWC compared to the RO community (Table S3). We found no significant differences in soil mineral N (NH_4, $NO_{3)}$, or air temperature between sites.

Discussion

Our first objective of this investigation was to determine if N biochemistry fractions could more accurately predict decomposition rate than bulk N alone. The majority of N fractions captured similar variation in decomposition explained by N_{mass} across the entirety of our experiment (Table 2, 3). Of the N fractions studied, only leaf chlorophyll explained variation unrepresented by N_{mass} – however, this trait was not found to be a significant predictor of decomposition rates according to our multiple regression.

Our second objective was to determine what green leaf traits could be used to predict decomposition rate. Similar to observations in the literature, leaf traits associated with photosynthetic capability (N_{mass}, amino acid, total protein) and structural integrity (LMA, lignin) explained a significant proportion of the variation in decomposition rate (Santiago 2007). Many of these parameters are well represented in trait databases and can be used explain variations in

decomposition rate for modeling purposes. To further support our conclusions, relationships between leaf traits and rates of decomposition should be examined in a larger, taxonomically diverse group of species through more advanced stages of decay.

Trait patterns and predictors

Green leaf traits generally aligned along a single axis of variation characteristic of the 'leaf economic spectrum' (LES, Wright et al. 2004), with structural, C-affiliated traits (LMA, lignin) opposing photosynthetic, N-affiliated traits (Table 2, Figure S1). This axis represented leaf traits that had the most predictive power within the scope of this study, with LMA and lignin opposing N_{mass} and other N biochemistry variables (i.e., amino acid concentration, and total protein). In live plants, lignin provides cell walls with structure and rigidity; in senesced litter, lignin has 'afterlife' effects, behaving as a structural barrier to decomposers and inhibiting access to more labile, N-rich components (reviewed in Austin and Ballaré 2010). LMA is likely the most notable trait to embody this axis of variation because it encapsulates the LES by representing the leaf dry mass (structure) to leaf area (photosynthetic capability), and is well represented in leaf trait databases (e.g. TRY, Kattge et al. 2011). Further, N fractions are difficult to measure, and easy-to-measure traits such as LMA may be more powerful predictors of litter decomposition rate.

The results of our PCA mirror patterns commonly seen in the literature which relate LES to rates of decomposition in regional and global studies (Cornwell et al. 2007, 2008, Santiago 2007, Bakker et al. 2011). Though leaf photosynthetic capability opposes LMA within the LES, we found these two traits to fall on different axes of variation within our PCA. This result is likely due to the limited size of this nine species study – species such as *P. canariensis*,

which contained relatively high N content and low photosynthetic capability may have been responsible for A_{area} aligning on an orthogonal axis. The LES axis is clearly observed within leaf traits but is less discernable among litter traits (Table 2), and LES-associated leaf traits were generally more powerful predictors of decomposition rate than comparable litter traits (Table 2,3). This observation may be attributed to conservation strategies during leaf senescence, where a significant proportion of leaf N is resorbed by the plant. This is evident in our results, as C:N values were relatively higher and N-associated traits were relatively lower (e.g., N_{mass}, soluble protein, membrane protein, cell wall protein, nucleic acid, amino acid) when measured as litter traits as opposed to leaf traits. This nutrient resorption may distort the axis associated with carbon-nitrogen trade-off, making the leaf economic spectrum less discernable among litter traits.

We found phenolics concentration to be a strong predictor of decomposition rate as a *litter* trait within this study, opposing litter N_{mass} in PC1. In live tissue, phenolics protect plants against herbivory and parasitism (Kuiters 1990). In litter, phenolics slow decomposition rate due to the formation of polyphenol-protein complexes, which are slow to biodegrade (so-called 'brown pigments', Kuiters 1990),. and may make litter N inaccessible to decomposers. Thus, a spectrum of variation in litter traits represented by phenolics concentration on one side and N_{mass} on the other may be more informative than measuring traditional LES traits in litter.

Site and species differences

Sites differed significantly in soil temperature, water content, extractable N, and organic matter. However, rates of decomposition more consistently differed among species, regardless of environmental conditions. Differences in

decomposition rates among species is not surprising, as our study focused on nine species of highly contrasting traits. When rates of decomposition differed significantly among sites, faster rates of decomposition were observed in the CSS community. CSS decomposition rate may have been higher due to comparably higher soil temperatures. However, continuous microclimate data collection was outside of the scope of this study and was not accounted for in our model.

Study Limitations

Recent studies highlight the important role that microclimate and intraspecific variation in leaf chemistry play in litter and wood decomposition. Bradford et al. (2016) argues that these cofactors, which were outside the scope of this study, could control decomposition rates independently of litter quality and climate at regional scales. Future decomposition studies should be designed in a way that maximizes replicates and captures within-site climate variability. In this study, we compared site-level aggregated climate data to rates of decomposition. Furthermore, our study included species that are not native to southern California CSS and RO communities. An investigation exclusively using native species might be more informative, as feedback mechanisms between a species' litter and the local decomposer community are likely to be more established (Allison et al., 2013; Ayres et al., 2009). While our study followed decomposition dynamics for 1.5 years, we also note the possibility that different traits may become stronger predictors of decomposition at more advanced stages of decay.

Conclusions

We found no evidence that N biochemical fractions could explain variation already explained by bulk estimation parameters such as LMA or

N_{mass}. However, our study highlights the ability of green leaf traits to accurately predict rates of decomposition. These results suggest that leaf trait databases can provide insight into rates of decomposition where litter chemistry data are not readily available.

Using methodology from Cornwell and Weedon 2014, we replaced the classic exponential decay model with the Weibull residence model. We suggest that future decomposition studies consider fitting this model to their species-site litter cohorts, as the Weibull model allows for much more flexibility in both slope and shape along the decomposition curve. We support recommendations made by these authors to replace the classic *k* metric with the half-life ($t_{1/2}$) parameter and the mean residence time ($\overline{t}$) of litter cohorts (*see* supplementary material, Cornwell and Weedon 2014). However, we note that these metrics should only be used if litter cohorts are allotted the appropriate time for more advanced stages of decomposition to occur.

Declarations

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• Authors' Contributions – JF and JK designed methodology. MR analyzed data and was the primary author. All authors collected data, analyzed data, contributed to writing, and gave approval for publication.

Conflicts of interest – The authors have no conflicts of interest to disclose.

Permits – Permits were assigned by the Irvine Regional Park for the field portion of our experiment.

Data Accessibility

Raw data will be published in a Zenodo repository upon manuscript acceptance.

References

Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? - J. Ecol. 84

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. - Oikos 79: 439–449.

Akaike, H. 1998. A new look at the statistical model identification. - In: Parzen, E. et al. (eds), Selected papers of Hirotugu Akaike. Springer New York, pp. 215–222.

Allison, S. D. et al. 2010. Resistance of microbial and soil properties to warming treatment seven years after boreal fire. - Soil Biol. Biochem. 42: 1872–1878.

Allison, S. D. et al. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. - Ecology 94: 714–725.

AOAC 1950. Official methods of analysis of the Association of Official Agricultural Chemists.

Austin, A. T. and Ballaré, C. L. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. - Proc. Natl. Acad. Sci. U. S. A. 107: 4618–4622.

Ayres, E. et al. 2009. Home-field advantage accelerates leaf litter decomposition in forests. - Soil Biol. Biochem. 41: 606–610.

Bakker, M. A. et al. 2011. Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. - Funct. Ecol. 25: 473–483.

Berg, B. and Staaf, H. 1980. Decomposition rate and chemical changes of scots pine needle litter. - Oikos: 373–390.

Berg, B. and 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. - Can. J. Bot. 69: 1449–1456.

Bonan, G. B. et al. 2013. Evaluating litter decomposition in earth system models with long-term litterbag experiments: An example using the Community Land Model version 4 (CLM4). - Glob. Chang. Biol. 19: 957–974.

Bradford, M. A. et al. 2016. Understanding the dominant controls on litter decomposition. - J. Ecol. 104: 229–238.

Bronk, D. et al. 2000. Total dissolved nitrogen analysis: Comparisons between the persulfate, UV and high temperature oxidation methods.

Chapin, F. S. and Kedrowski, R. A. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. - Ecology 64: 376–391.

Cornwell, W. K. and Weedon, J. T. 2014. Decomposition trajectories of diverse litter types: A model selection analysis. - Methods Ecol. Evol. 5: 173–182.

Cornwell, W. K. et al. 2007. The leaf economic spectrum drives litter decomposition within regional floras worldwide. - Ecol. Lett. 11: 1065–1071.

Cornwell, W. K. et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. - Ecol. Lett. 11: 1065–1071.

Dyer, M. L. et al. 1990. Apparent controls of mass loss rate of leaf litter on a regional scale. - Scand. J. For. Res. 5: 311–323.

Funk, J. L. 2005. Hedychium gardnerianum invasion into Hawaiian montane rainforest: Interactions among litter quality, decomposition rate, and soil nitrogen availability. - Biogeochemistry 76: 441–451.

Funk, J. L. et al. 2013. Differential allocation to photosynthetic and non-photosynthetic nitrogen fractions among native and invasive species. - PLoS One 8: 1–10.

Kattge, J. et al. 2011. TRY - a global database of plant traits. - Glob. Chang. Biol. 17: 2905–2935.

Kuiters, A. T. 1990. Role of phenolic substances from decomposing forest litter in plant-soil interactions. - Acta Bot. Neerl. 39: 329–348.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. - Ecology 59: 465–472.

Melillo, J. M. et al. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. - Ecology 63: 621–626.

Noctor, G. et al. 2002. Co-ordination of leaf minor amino acid contents in crop species: significance and interpretation. - J. Exp. Bot. 53: 939–945.

Noctor, G. et al. 2007. A comparative study of amino acid measurement in leaf extracts by gas chromatography-time of flight-mass spectrometry and high performance liquid chromatography with fluorescence detection. - Metabolomics 3: 161–174.

Pietsch, K. A. et al. 2014. Global relationship of wood and leaf litter decomposability: The role of functional traits within and across plant organs. - Glob. Ecol. Biogeogr. 23: 1046–1057.

Rahman, M. M. et al. 2013. Lignin and its effects on litter decomposition in forest ecosystems. - Chem. Ecol. 29: 540–553.

Raich, J. W. and Schlesinger, W. H. 1992. The global carbon dioxide flux in soil

respiration and its relationship to vegetation and climate. - Tellus B 44: 81–99.

Rovira, P. and Vallejo, V. R. 2002. Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: an acid hydrolysis approach. - Geoderma 107: 109–141.

Santiago, L. S. 2007. Extending the leaf economics spectrum to decomposition: Evidence from a tropical forest. - Ecology 88: 1126–1131.

Scott, N. A. and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. - Oecologia 111: 151–159.

Strickland, M. S. et al. 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. - Funct. Ecol. 23: 627–636.

Sun, S. W. et al. 2006. Efficiency improvements on ninhydrin method for amino acid quantification.

Swift, M. J. and Anderson, J. M. 1989. Chapter 31 - Decomposition. - In: Werger (ed), Ecosystems of the World. Elsevier, pp. 547–569.

Takashima, T. et al. 2004. Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous Quercus species. - Plant, Cell Environ. 27: 1047–1054.

Terashima, I. and Evans, J. R. 1988. Effects of light and nitrogen nutrition on the organization of the photosynthetic apparatus in spinach. - Plant Cell Physiol. 29: 143–155.

Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. - Nature 428: 821–827.

Zhang, D. et al. 2008. Rates of litter decomposition in terrestrial ecosystems:

global patterns and controlling factors. - J. Plant Ecol. 1: 85–93.

Appendix 1

Figure A1. The first, second, third and fourth axes from PCA. Arrows indicate direction and weighing of vectors representing seven (litter) and eight (leaf) traits. Points are species means. Only traits which load strongly on one of the displayed axes are labelled alongside vectors. Trait abbreviations are provided in the text.

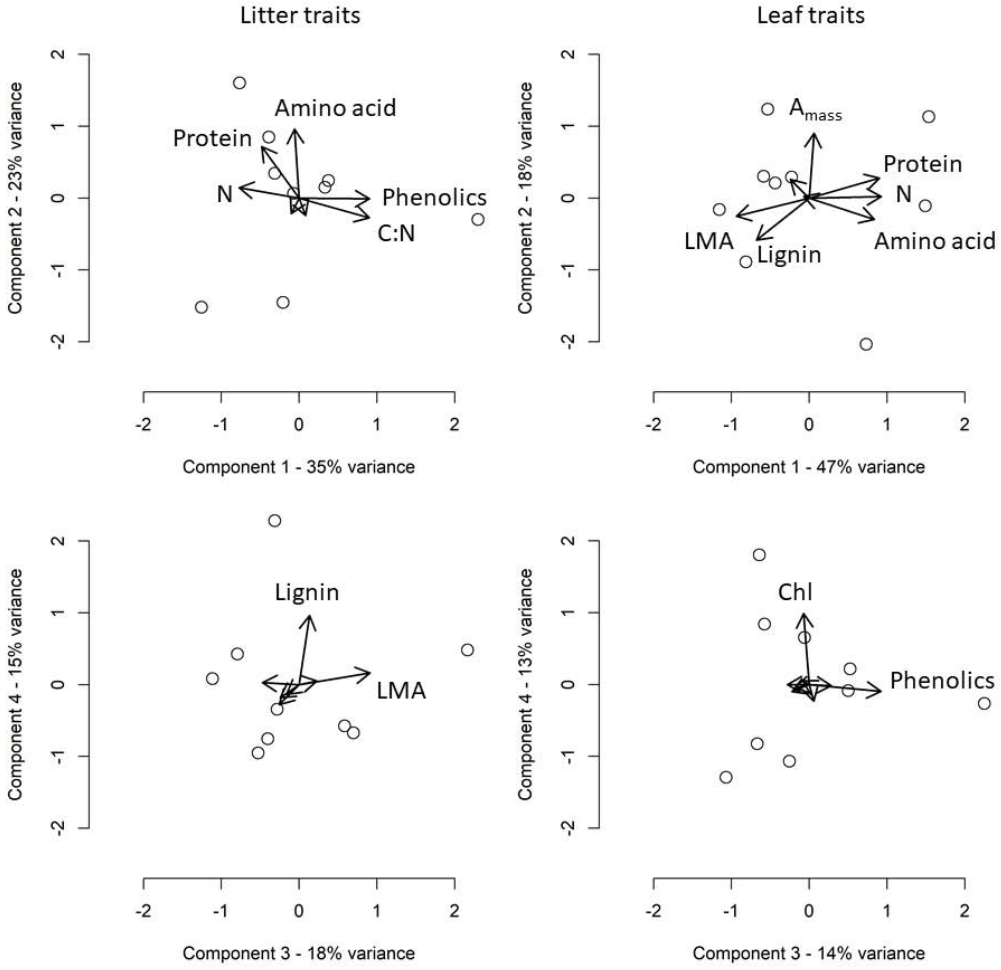

Figure A2: Species differences in mass loss for nine species at six time points (0.1, 0.3, 0.5, 0.8, 1.0, and 1.5 years). Species means (n=10) with the same uppercase letter are not significantly different from each other at $P < 0.05$.

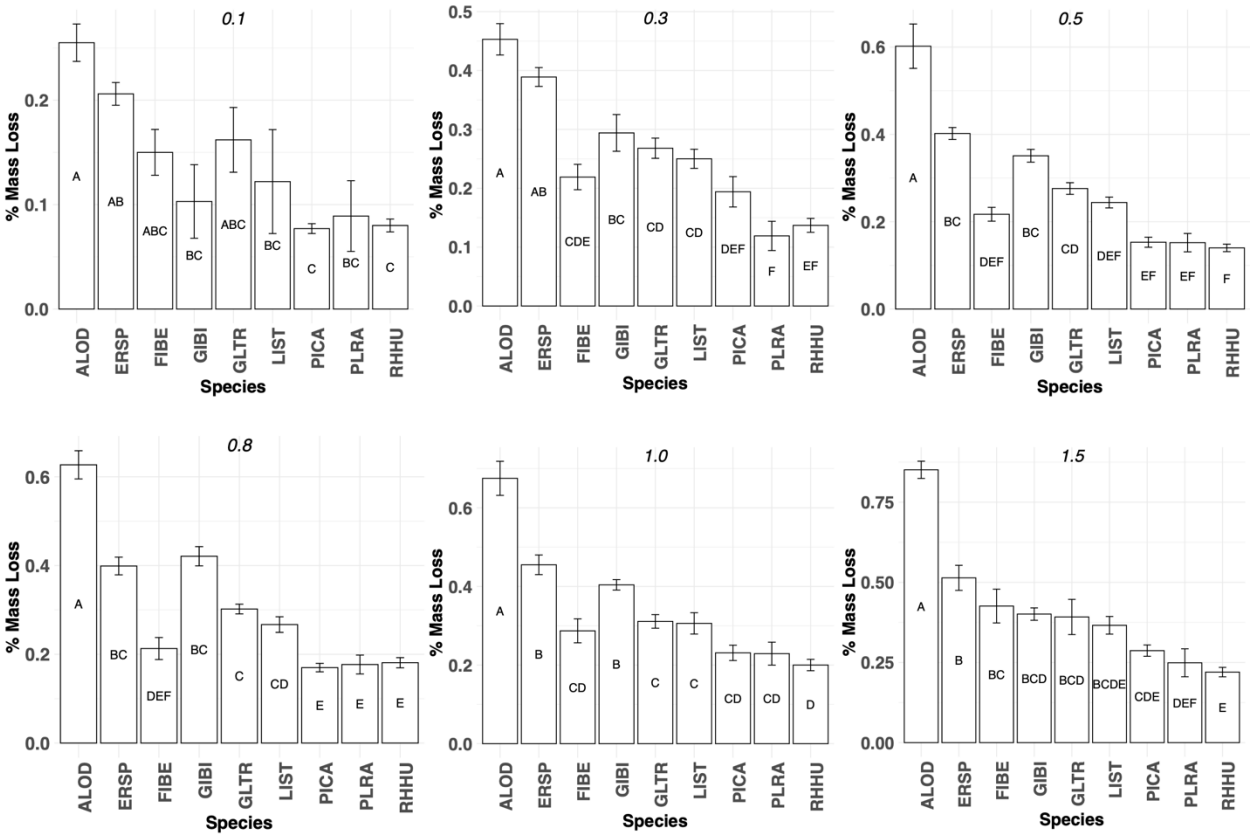

Table A1. Results from a two-way ANOVA, with site (CSS or RO) and species as factors and mass loss as the dependent variable. Significant ($P < 0.05$) results are bolded. When SITE was significant, CSS communities displayed higher decomposition rate.

Time (yr)	Factor	df	F	P
0.1	SITE	1	0.009	0.924
	SPECIES	**8**	**4.89**	**<0.001**
	SITE:SPECIES	8	0.98	0.46
	Residuals	72		
0.3	SITE	1	3.79	0.056
	SPECIES	**8**	**27.04**	**<0.001**
	SITE:SPECIES	8	1.61	0.14
	Residuals	72		
0.5	SITE	1	0.912	0.34
	SPECIES	**8**	**50.02**	**<0.001**
	SITE:SPECIES	8	0.59	0.78
	Residuals	72		
0.8	**SITE**	1	**34.35**	**<0.001**
	SPECIES	**8**	**79.28**	**<0.001**
	SITE:SPECIES	8	0.52	0.84
	Residuals	72		
1	**SITE**	1	**61.04**	**<0.001**
	SPECIES	**8**	**58.27**	**<0.001**
	SITE:SPECIES	8	1.29	0.26
	Residuals	72		
1.5	SITE	1	0.53	0.47
	SPECIES	**8**	**26.24**	**<0.001**
	SITE:SPECIES	8	0.94	0.49
	Residuals	72		

Table A2. Leaf biochemical traits for green leaves and litter in nine species. All measures are expressed per gram of dry weight. Data are means with standard error in parentheses. Samples from multiple leaves were combined for LMA and lignin analysis; thus, no standard error is reported. Species abbreviations in Table 1.

Species	Type	LMA	N_{mass}	C:N	Lignin	Lignin:N	Total phenolics	Soluble protein	Membrane protein	Cell wall protein	Nucleic acid	Amino acid
		g m^{-2}	%	g g^{-1}	%	g g^{-1}	%	mg g^{-1}	mg g^{-1}	mg g^{-1}	mgN g^{-1}	mgN g^{-1}
ALOD	Leaf	34.9	3.5 (0.0)	12.5 (0.1)	1.4	26.9	3.6 (0.1)	354 (27)	203 (50)	45.1 (6.5)	3.42 (0.51)	2.45 (0.22)
	Litter	36.5	1.0 (0.1)	39.6 (4.3)	7.9	7.9	5.1 (0.6)	43.7 (4.2)	32.0 (10.5)	14.1 (2.2)	0.24 (0.05)	0.62 (0.08)
ERSP	Leaf	40.3	4.6 (0.1)	10.1 (0.2)	9.2	0.4	5.7 (0.3)	407 (47)	139 (33)	19.7 (6.8)	1.70 (0.16)	1.79 (0.22)
	Litter	64.6	1.6 (0.0)	27.5 (1.0)	12.6	7.9	5.9 (0.5)	44.3 (6.7)	50.9 (6.2)	15.2 (1.9)	0.39 (0.06)	0.75 (0.08)
FIBE	Leaf	153.8	1.6 (0.0)	28.6 (0.3)	15.8	7.9	3.8 (0.1)	117 (13)	26.2 (3.6)	6.9 (1.2)	0.78 (0.11)	0.38 (0.05)
	Litter	103.9	0.5 (0.0)	87.6 (2.9)	16.5	31.2	3.7 (0.2)	13.4 (1.5)	4.9 (1.0)	1.4 (0.5)	0.14 (0.02)	0.09 (0.02)
GIBI	Leaf	101.5	1.8 (0.2)	25.8 (2.6)	9.3	2.0	7.8 (0.5)	8.0 (2.3)	135 (7)	32.5 (7.1)	1.73 (0.27)	0.74 (0.12)
	Litter	107.1	1.1 (0.1)	39.0 (2.4)	12.2	10.9	9.0 (0.6)	2.9 (0.6)	23.1 (1.8)	7.3 (1.4)	0.26 (0.02)	0.58 (0.07)
GLTR	Leaf	113.1	1.7 (0.1)	29.4 (1.0)	13.8	7.9	13.6 (1.4)	134 (10)	44.9 (6.8)	34.7 (4.7)	1.58 (0.22)	0.62 (0.19)
	Litter	54.2	0.9 (0.0)	54.6 (2.7)	19.7	22.0	12.9 (0.2)	17.3 (4.0)	7.1 (2.9)	6.6 (2.9)	0.20 (0.00)	0.53 (0.09)
LIST	Leaf	110.2	1.1 (0.2)	43.2 (5.0)	12.45	11.1	23.2 (4.0)	51.1 (13.1)	24.2 (2.0)	12.0 (0.3)	0.51 (0.01)	0.15 (0.00)
	Litter	86.0	0.3 (0.1)	158 (42)	9.4	26.9	31.2 (5.2)	11.1 (1.6)	1.5 (0.2)	0.9 (0.2)	0.16 (0.00)	0.36 (0.06)
PICA	Leaf	167.3	1.2 (0.1)	41.4 (2.4)	15.9	9.8	4.7 (1.1)	1.0 (0.3)	91.2 (15.4)	15.6 (0.8)	0.19 (0.02)	0.78 (0.09)
	Litter	169.7	0.6 (0.1)	86.4 (18.0)	25.4	41.6	5.0 (0.2)	5.9 (2.4)	13.8 (4.3)	5.7 (0.7)	0.18 (0.02)	0.34 (0.03)
PLRA	Leaf	102.8	1.7 (0.0)	28.5 (0.4)	15.8	5.2	5.0 (0.3)	22.5 (8.2)	113 (9)	56.5 (8.0)	0.54 (0.05)	0.67 (0.11)
	Litter	83.4	0.9 (0.5)	85.9 (31.5)	38.0	42.6	7.5 (1.9)	3.9 (0.8)	17.5 (2.7)	6.0 (2.1)	0.21 (0.04)	0.38 (0.05)
RHHU	Leaf	91.5	2.5 (0.1)	19.5 (0.5)	17.1	8.2	5.7 (0.5)	86.6 (21.6)	109 (21)	21.9 (1.5)	0.79 (0.10)	2.75 (0.29)
	Litter	70.7	1.8 (0.4)	27.6 (5.8)	21.7	11.9	5.0 (0.9)	13.9 (0.9)	15.8 (7.0)	5.5 (1.0)	0.18 (0.02)	0.17 (0.03)

Table A3. Environmental characteristics of the two study sites (CSS, coastal sage scrub; RO, riparian oak woodland). Data are means across time points (standard error in parentheses). Degrees of freedom (df) and t statistic (unpaired student's t-test) are shown. Statistically significant differences between the sites are noted at $P < 0.05$ (**bolded**). GWC is gravimetric water content.

Measured Characteristic	CSS	RO	df	t
Air Temp (°C)	28.3 (3.7)	24.5 (2.3)	10	0.88
Soil Temp (°C)	27.3 (2.0)	18.1 (0.6)	30	**4.31**
GWC (%)	7.2 (1.2)	15.0 (1.4)	58	**4.30**
NH4 (μg NH_4-N g dry $soil^{-1}$)	4.2 (0.6)	12.0 (3.6)	8	2.11
NO3 (μg NO_3-N g dry $soil^{-1}$)	3.5 (0.8)	7.0 (2.9)	8	1.18
Total Extractable N (μg N g dry $soil^{-1}$)	7.7 (1.1)	19.0 (1.4)	8	**6.38**
Organic Matter (%)	3.4 (0.1)	7.7 (1.4)	8	**3.14**

Figure Legends

Figure 1. Average decomposition rate for each species-site combination. Points represent proportion of mass loss among replicates (n=5) for the CSS site (red) and RO site (blue). Error bars are standard error. Each species-site combination was fitted with a Weibull distribution model are represented as curves.

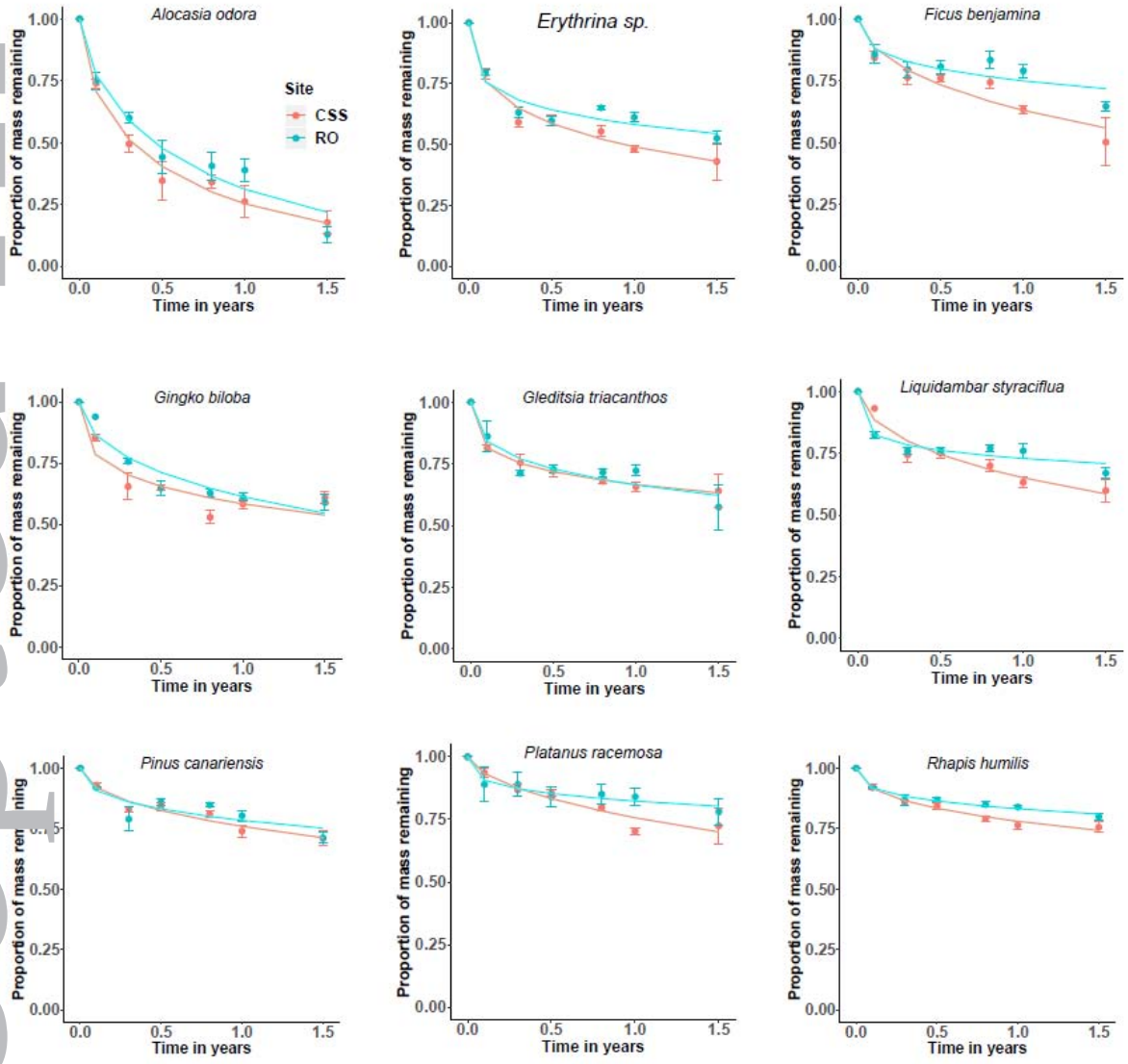

Figure 2. Pearson correlations for (a) leaf and (b) litter traits.

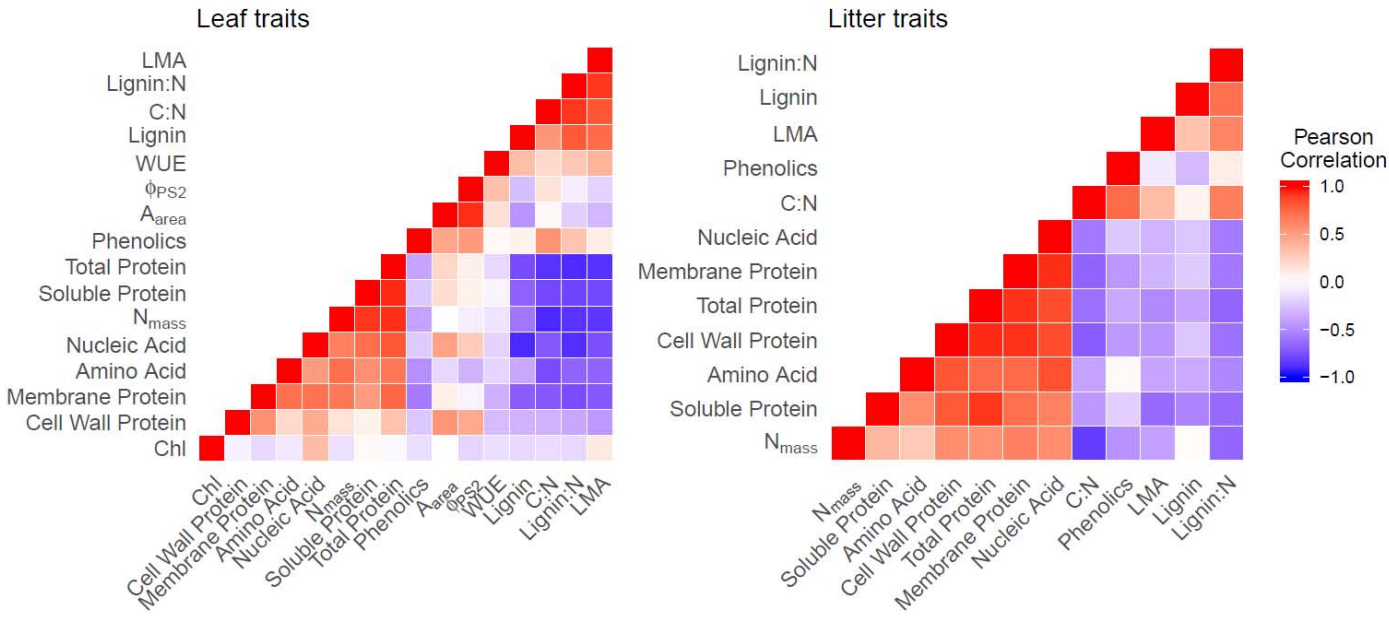

Table Legends

Table 1. Plant species used for the decomposition experiment and their leaf-level physiology traits. Data are means across five replicate individuals, with standard error in parentheses. * = nitrogen-fixing species. † = species native to southern California

Code	Species	Common Name	Deciduous/ evergreen	A_{area}	WUE	ΦPSII	Chl
ALOD	*Alocasia odora*	Elephant ear	Evergreen	20.6 (0.9)	4.75 (0.27)	0.115 (0.006)	796 (161)
ERSP	*Erythrina sp.*	Erythrina*	Evergreen	11.0 (1.8)	7.28 (0.21)	0.108 (0.013)	278 (48)
FIBE	*Ficus benjamina*	Weeping fig	Evergreen	4.4 (0.4)	6.44 (1.53)	0.035 (0.004)	1297 (208)
GIBI	*Gingko biloba*	Gingko	Deciduous	13.4 (1.9)	6.04 (0.78)	0.114 (0.015)	729 (74)
GLTR	*Gleditsia triacanthos*	Honey locust*	Deciduous	26.8 (3.6)	9.90 (0.28)	0.203 (0.013)	684 (35)
LIST	*Liquidambar styraciflua*	American sweetgum	Deciduous	17.1 (2.5)	5.14 (0.50)	0.132 (0.031)	414 (30)
PICA	*Pinus canariensis*	Canary Island pine	Evergreen	9.3 (1.1)	8.81 (2.25)	0.090 (0.010)	248 (34)
PLRA	*Platanus racemosa*	California sycamore†	Deciduous	15.0 (2.6)	4.81 (0.10)	0.120 (0.021)	374 (35)
RHHU	*Rhapis humilis*	Reed palm	Evergreen	4.7 (0.6)	6.24 (0.31)	0.036 (0.001)	503 (99)

Trait abbreviations: Area-based photosynthetic rate (A_{area}, μmol m^{-2} s^{-1}); water-use efficiency (WUE, μmol CO_2 mmol H_2O^{-1}); effective quantum yield of Photosystem II (ΦPSII, $\Delta F/F'_m$); and leaf chlorophyll content (Chl, μmol m^{-2}).

Table 2. Standardized loadings for four principal components from PCA. Primary associations of each trait with the four axes are bolded. Trait abbreviations are provided in the text.

	Leaf traits				Litter traits			
	PC 1	PC 2	PC 3	PC 4	PC 1	PC 2	PC 3	PC 4
A_{area}	0.06	**0.90**	0.28	-0.02				
Chl	-0.07	0.03	-0.07	**0.99**				
N_{mass}	**0.92**	0.02	-0.22	-0.10	**-0.77**	0.14	-0.47	0.03
C.N					**0.90**	-0.27	0.23	0.05
LMA	**-0.94**	-0.25	-0.08	0.05	0.08	-0.24	**0.91**	0.16
Lignin	**-0.68**	-0.58	0.06	-0.23	-0.10	-0.21	0.13	**0.96**
Phenolics	-0.24	0.26	**0.92**	-0.09	**0.90**	-0.01	-0.24	-0.18
Total Protein	**0.90**	0.28	-0.28	0.00	-0.48	**0.72**	-0.26	-0.28
Amino Acid	**0.83**	-0.30	-0.19	-0.05	-0.06	**0.96**	-0.16	-0.14

Table 3. Weibull model-predicted decomposition values as a function of principal components for leaf and litter traits in coastal sage scrub and riparian oak communities at six time points (0.1, 0.3, 0.5, 0.8, 1.0, and 1.5 years). Only significant t-values from the multiple regression are included. See Table 2 for traits associated with each PC axis.

A. Leaf traits	Coastal Sage Scrub						Riparian Oak					
	0.1	0.3	0.5	0.8	1.0	1.5	0.1	0.3	0.5	0.8	1.0	1.5
Intercept	60.86	46.17	35.44	26.48	22.92	17.62	63.65	53.86	43.30	33.33	29.27	23.27
PC 1	-3.77	-4.91	-4.73	-4.28	-4.02	-3.52	-2.79	-4.40	-4.65	-4.52	-4.39	-4.11
PC 2	-3.05	-3.70	-3.49	-3.11	-2.91	-2.54			-4.05	-4.04	-3.98	-3.83
PC 3												
PC 4												
Adjusted R^2	0.74	0.83	0.82	0.79	0.76	0.70		0.80	0.82	0.82	0.82	0.80

B. Litter traits	Coastal Sage Scrub						Riparian Oak					
	0.1	0.3	0.5	0.8	1.0	1.5	0.1	0.3	0.5	0.8	1.0	1.5
Intercept	60.05	48.87	24.44	35.90	32.72	27.07	67.54	66.40	59.39	48.38	42.84	33.82
PC 1	-2.88	-4.76	-5.53	-5.95	-6.01	-5.90		-5.38	-6.79	-7.32	-7.3	-6.97
PC 2												
PC 3												
PC 4	4.11	5.03	5.23	5.13	4.98	4.57		4.92	5.85	6.11	6.05	5.80
Adjusted R^2	0.73	0.85	0.87	0.88	0.88	0.87		0.87	0.91	0.91	0.92	0.91