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Dynamics of necromass in woody Australian ecosystems

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Abstract. Litterfall (LF) is the major contributor to aboveground necromass in ecosystems. Litter decomposition or litter decay (LD) then offsets deposition in LF, with the balance of LF and LD determining the standing litter (SL). SL together with fine and coarse woody debris (FWD, CWD) are the largest necromass pools. The interactions of LF, SL, and LD at continental scales reflect carbon and nutrient cycling and other ecosystem processes. We compiled data on leaf, twig (<2.6 cm), and other material (mostly bark and reproductive tissue) for SL and LF for the fire-prone Australian continent, where SL is also a major "fuel load" and important for fire spread and fire intensity. We extracted data from 498 published and unpublished works (1825 LF observations; n SL = 3914; n LD = 629). We used Olson's (mass-balance) approach (k ~ LF/SL) to calculate LD for sites long undisturbed with both LF and SL data. We compiled LF and SL by component (leaves, twigs, other material) and metainformation such as sampling location, tree species, or time since fire from literature and/or scientists. Most data were available from warm-seasonal (36% for SL) and cool-wet (31%) climates, linking the locations of our data with a bio-climate classification. Warm-wet (20%) and hot-seasonal (8%) climates followed, while other climate zones each contributed <2% of the data. Across all climatic zones, average SL (1100 g/m^2) was roughly twice that of LF (468 $g \cdot m^{-2} \cdot yr^{-1}$). SL was greatest in cold climates (2334 g/m^2), compared to warm-wet (1168 g/m^2) and hot-seasonal conditions (499 g/m^2). Important drivers of SL are LD (e.g., slow under cold conditions) and fire frequency. Olson's k varied with type of decomposing material ("composition"). For example, across the continent, k ~ 1.942 yr^{-1} for leaves but was 0.504 yr^{-1} for twigs. SL varied strongly in composition according to climate type (e.g., seasonal vs. wet climates). Robust models of necromass dynamics must distinguish between the litter components (such as leaves and twigs) and consider the complex and non-linear effects of climate, stand structure, and stand history on litterfall and decomposition.

Key words: Acacia; carbon sequestration; Eucalyptus; fire risk; forest floor; fuel load; nutrient cycling; rainforest; soil organic matter; woodland.

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Introduction

Litterfall (LF) is a critical process in nutrient cycling, transferring carbon and nutrients from the vegetation to the litter layer on the soil surface. Along with belowground root turnover and fall of woody debris (branch shedding and/or tree mortality, usually >2.5 cm), the shedding of material <2.5 cm (i.e., leaves, needles, small twigs, bark, reproductive material) is the major mechanism for adding necromass to soils and contributes the major component of non-living fuel loads in forests and other ecosystems (Vitousek 1984, Malhi et al. 2011). The term coarse woody debris (CWD) is usually used for material larger than 10 cm (or 7.6 cm at smaller end in the United States) and material between 2.5 and 7.6 is called medium fine woody debris (FWD), if considered at all (Harmon et al. 1986, Woodall et al. 2013, Puletti et al. 2019). Necromass on the forest floor (or standing litter, SL) is a widely used measure of fuel load (Gould et al. 2011), while LF (deposition or input) and litter decomposition (decay or output, LD) determine its rate of increase. Deposition and decomposition largely control SL, in addition to disturbances (Keane 2015). The balance between inputs and outputs varies depending on interactions among stand age (Turner and Lambert 2002), basal area (Keane 2008), climate (Liu et al. 2004), and stand density and remotely sensed leaf area index (Neumann et al. 2018). A significant limitation of available literature in Australia is that it has not been synthesized on continental scale and models of necromass dynamics thus focus on single ecosystems or single dominant species (Turner and Lambert 2002, Thomas et al. 2014).

SL also constitutes a significant proportion (˜5–7%) of overall forest carbon (C) (Pan et al. 2011). LF equals about one third of net primary production (NPP) in large areas of forests in Europe and the Americas (Cleve et al. 1983, Malhi et al. 2011, Risch et al. 2012, Neumann et al. 2018), yet we have limited information on contributions of LF to the carbon cycle elsewhere. Combining data on LF and SL offer potential insights into LD (important for carbon assessments) as well as into the dynamics of fuel loads (important for fire risk). More information is available for SL than for LF due to the relative ease of sampling (and thus cost). LF is measured with traps that are emptied routinely with the contents dried and weighed. SL is commonly sampled within designated areas down to the mineral soil. For FWD and CWD, diameter and abundance are typically measured within transects, with conversion factors applied to scale to area (Woodall et al. 2013).

For LF, there are a few consistent and harmonized datasets available for large areas (e.g., Chave et al. 2010, Holland et al. 2015, Neumann et al. 2018). Continuous monitoring has been implemented in Europe and North America (Risch et al. 2012, Neumann et al. 2018). However for the Australian continent, there has been no collation of LF and SL observations, apart from modest efforts for carbon models (Paul and Polglase 2004, Roxburgh et al. 2015), and some regional analyses (Marsden-Smedley and Anderson 2011, Watson 2012). Analyses of economically important species (Turner and Lambert 2002) have not been extended to all types of woody vegetation. Considerable amounts of data on litter have been collected as part of fuel load assessments (e.g., for Tasmania Marsden-Smedley and Anderson (2011); for New South Wales Watson (2012), Thomas et al. (2014)), but these data are seldom used beyond developing models of fuel load, fire spread, or intensity (Keane 2015). Such data are usually classified according to location or fire risk (e.g., "fine fuel," "surface fuel," "elevated fuel," "1-hour fuel," or "10-hour fuel") and require careful interpretation (e.g., separation of litter components). The heterogeneity of litter (Burghouts et al. 1998) and the resulting range of definitions (Holland et al. 2015) also need careful consideration. For example, decomposition is a major driver of litter accumulation and leaf and non-leaf material decompose at rates that differ by an order-of-magnitude, yet are lumped together in some fuel load assessments.

We sought to synthesize a consistent dataset for continental-scale analysis of the dynamics of necromass (including LF, LD, and SL) across Australia. Broadly, and based on the literature, we hypothesized that the driving influences on LF and SL would be similar but that greater climate seasonality would increase SL. Our objectives (and implied specific hypotheses) were thus:

1. Test whether variation in climate at regional (e.g., bio-climatic zones) and continental scale could account for observed variation in LF and SL;
2. Test whether fire history and vegetation structure help determine SL through their effects on LF and LD; and
3. Test whether type of litter material (leaf vs. wood) helps explain variation in SL not

explained by site (e.g., climate) and stand (e.g., vegetation structure) conditions.

Material and Methods

Collating and harmonizing data

We complemented existing LF and SL datasets (Turner and Lambert 2002, Thomas et al. 2014, Holland et al. 2015) with recent studies and data not previously considered. We used research databases and journal websites to identify potential sources of information and consulted with scientists currently and previously involved in litter studies in Australia, to obtain unpublished data (e.g., from unpublished observations, student theses). We considered all terrestrial woody vegetation, including native forests and woodlands, but also plantations, afforestation of various designs and purposes, mangroves, natural shrublands, and savannas. We excluded aquatic systems (i.e., streams), grassland, cropland, and other intensive agriculture. We also excluded modeled LF and SL and studies based on visual estimates of fuel depth, as these are prone to substantial errors (Volkova et al. 2016).

Data for necromass (LF and SL) were classified into leaves (including phyllodes for *Acacia* spp.), twigs (<2.6 cm), bark, reproductive material, and fragments. Most litter trap designs were insufficient to capture the variability of larger wood (e.g., due to tree mortality or partial mortality) or to measure LF from grassy or herbaceous understories. We separated grass or herbaceous LF, if measured. Woody material <2.6 cm diameter was included with twigs and >2.6 cm diameter was included as "coarse woody debris" (CWD) or "CWD fall." For studies that used a smaller diameter threshold (usually 0.6 or 1 cm), we assigned a "fine fuel" code. Where we could not determine the share of twigs or bark, we avoided speculative assumptions and only used total SL and LF. For SL, we used "charcoal" as an additional class. We considered separately "CWD fall" and "CWD," to ensure that the definition of LF collected by traps can be directly compared to SL (including twigs up to 2–2.6 cm, depending on study). Likewise, when we used reports of fuel loads for quantification of necromass, we excluded shrubs, grasses, and other understory. These were included as a separate category. We excluded studies where we could not separate grass and understory (near-surface or elevated fuel layers) from SL (e.g., fuel studies such as Fensham [1992], McColl-Gausden and Penman [2017]). If data on the mass of dead standing trees were reported, we added this information as an additional class.

In many European and North American studies, SL is considered to be equivalent to an organic soil horizon (Zanella et al. 2011), while fuel studies consider fine organic material as "duff" (Gould et al. 2011, Lydersen et al. 2015). In many of these studies, identifiable plant material in the organic horizon is further separated into three layers, L, F, and H (Klinka et al. 1997). In our study of Australian ecosystems where humus layers (which lack identifiable plant tissues) are often vanishingly small and contaminated with soil particles and roots (Zanella et al. 2011), litter components such as leaves, bark, or twigs represent the L layer. Fragmented and partly decomposed necromass (in our database called "fragments") corresponds to the F layer. We separated humus (if present) from L + F on the basis of original reports. In some cases, it was necessary to recalculate published data to ensure consistency. SL used in this study represents L + F.

We collected metainformation including location, species, disturbance history, or stand information from related publications and contacting authors. Every site having a full year of LF measurements (g $m^{-2}\cdot yr^{-1}$) was considered as a single independent observation and combined with the respective measures of SL (multiple measurements averaged over one year).

Data analysis

LF data were paired with the appropriate SL data wherever possible. We then computed an estimate for LD (decay, turnover) using Olson's (1963) model (assumed equilibrium SL). The decomposition constant, *k,* is thus:

$$k = \mathrm{LF}/\mathrm{SL} \qquad ((1))$$

where LF is litterfall ($g\cdot m^{-2}\cdot yr^{-1}$) and SL is standing litter (g/m^2). We only calculated k ($year^{-1}$) for sites unburnt for at least five years and that were not irrigated and/or intensively fertilized. We calculated k for total LF, for leaf LF, and for twig LF (including bark, that is often pooled with twigs). Decomposition constants (k) derived in this way are not equivalent to rates of decomposition (also labeled k) derived from litter bag studies or exponential models (Krishna and Mohan 2017) and are dependent on a (questionable) assumption of steady state.

Commonly, descriptions of vegetation structure were incomplete, with at least one missing component. We used Eq. 2 to supplement missing data:

$$\mathrm{DBH} = (\mathrm{BA}/N \times 40,000/\pi)^{0.5} \quad (2)$$

where DBH is the quadratic mean diameter (cm), BA is the basal area (m^2/ha), and N is stem density (no./ha).

Fig. 1 shows the location of our observations on the Australian continent. We overlayed the locations with agro-climatic zones (Hutchinson et al. 2005) simplified into eight groups: cold, cool-wet, warm-wet, warm-seasonal, hot-wet, hot-seasonal, semiarid, and arid (Prior et al. 2011). Clearly, there is a heavy bias toward the warm-wet south-east, and a sampling bias to SL (Fig. 1). Nonetheless, observations encompass a wide range of climates and most of the continent. Western Australia (27% of SL observations) and New South Wales (20%) are the most strongly represented states, and cool-wet (36%) and warm-seasonal (31%) are the climatic zones with most SL observations. Inland regions are the least well represented.

We used consistent gridded data on climate and soils with the greatest available spatial resolution (30 arc seconds or 0.0083°) to ensure that subsequent statistical analyses were not affected by inconsistencies in the input data. We selected covariates to capture differences in vegetation structure, climate, soil, fire history, and location (Appendix S1: Table S1) and used them as

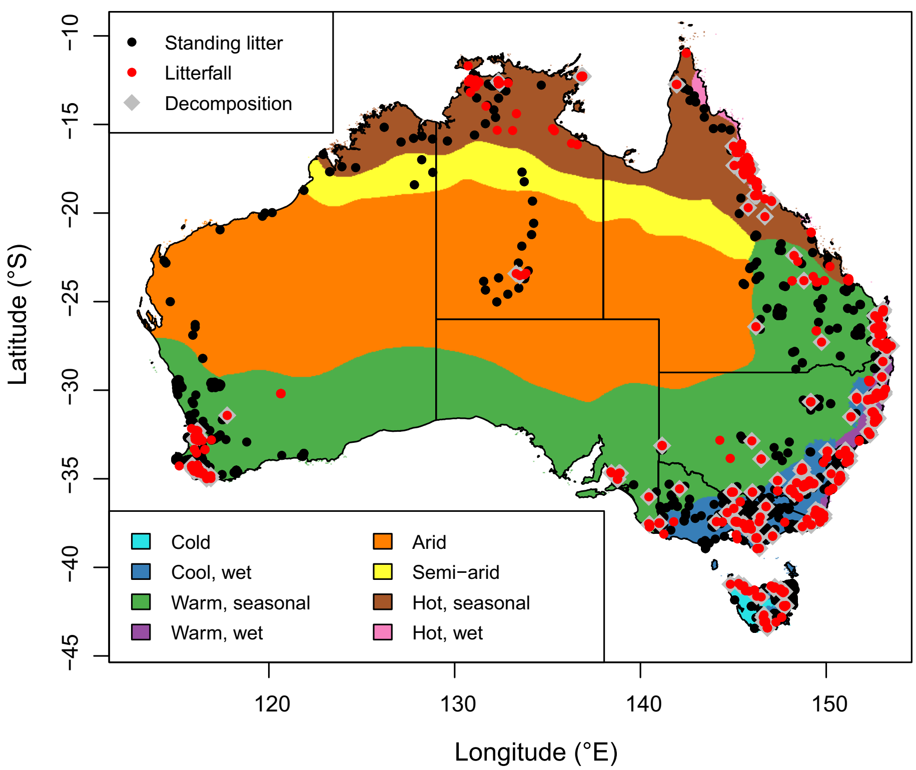

Fig. 1. Location of available data on litterfall (red), standing litter (black), and litter decomposition (gray, litterfall and standing litter measured for the same site) and bio-climatic zones (Hutchinson et al. 2005). Cold zone is in western Tasmania, hot-wet at coastal northern Queensland, and warm-wet at eastern Queensland and New South Wales.

covariates in single linear models to explore their effect on necromass components, LF, SL, and LD. We used annual LF and SL observations for model fitting. Covariates, on the other hand, were held constant over time. For example, we used average annual precipitation from 1970 to 2000 as our precipitation covariate. We did not consider seasonal climatic conditions, lag effects, or interaction terms, in order to retain a focused approach. We also tested multiple linear models for estimating SL using Bayes information criterion (BIC) for selecting the three most important covariates and controlling for overfitting (Calcagno and Mazancourt 2010). We considered second-degree polynomial covariates as means of exploring non-linear correlations and fitted models for leaf SL, wood SL, the L layer, the F layer, and the sum of L and F. All analyses and visualization were computed using the R language and environment (R Development Core Team 2016).

Results

A consistent continental necromass dataset

The collated data span more than half a century of collections from 498 individual studies conducted by a range of authors (see list of data sources; Appendix S1: Fig. S1). Collectively, the data reflect key ecosystem attributes at a hitherto unprecedented scale for the Australian continent (Fig. 2). More data were available for SL (n = 3914) than for LF (n = 1825), arguably due to the differences in effort required for their collection and analysis, and due to SL data being collected routinely as part of fuel assessments.

Across all Australian woody species (excluding tidal-affected mangroves and irrigated sites), average LF was 468 $g \cdot m^{-2} \cdot yr^{-1}$ with a standard deviation of 251 $g \cdot m^{-2} \cdot yr^{-1}$. SL was even more variable (1100 $\pm$ 982 g/m^2). These continental patterns of variation reflect variation at the species level (respective means, SDs; Table S2) and highlight that both LF and SL are subject to large spatial and temporal variability. Similarly, grouping the data by climatic zones revealed that SL decreased as conditions changed from cold to hot and arid (Fig. 2; Table S2). Thus, both LF and SL vary regionally and on continental scale by climate (objective 1). Both mean and variation of SL were greatest in cold (2334 $\pm$ 2459 g/m^2) and cool-wet climates (1279 $\pm$ 964 g/m^2). Mean SL was 10-15 folds less in arid (154 $\pm$ 173 g/m^2) and semiarid climates (111 $\pm$ 140 g/m^2). Like SL, LF declined with increasing aridity. In seasonal climates, LF was by about 300 $g \cdot m^{-2} \cdot yr^{-1}$ lower than if water availability was more constant throughout the year ("wet climates," Fig. 2; Appendix S1: Table S2).

Leaves and twigs contributed similarly to the L layer. SL used in subsequent analysis ("total litter" in Fig. 3) represents the L and F layers (i.e.,

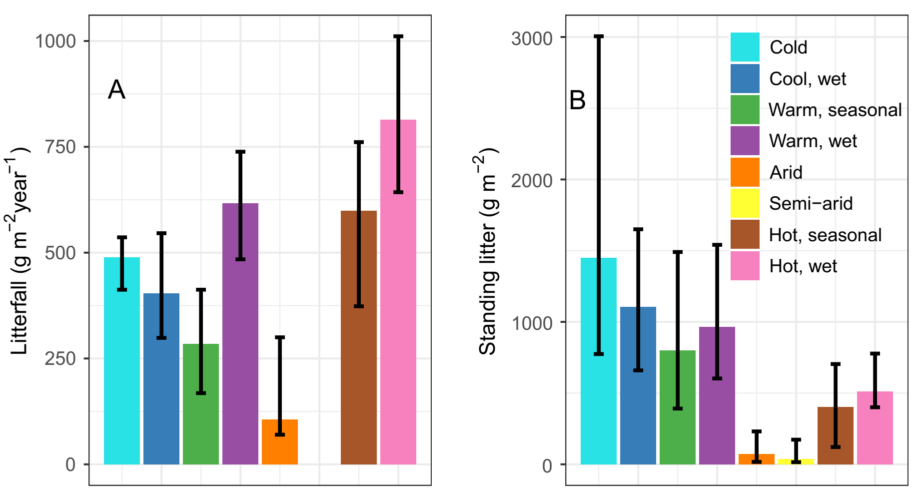

Fig. 2. Litterfall (A) and standing litter (B) by bio-climatic zone. The bars represent median and the vertical lines the interquartile range (25th to 75th quartile).

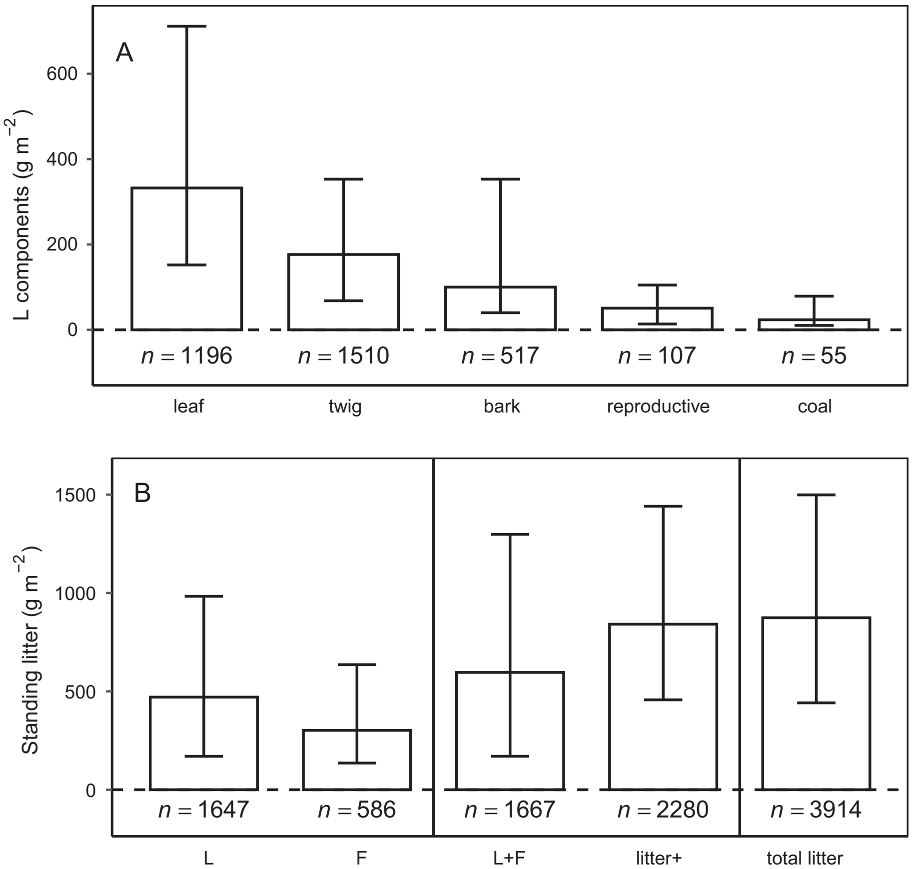

Fig. 3. Components of standing litter. We show in panel A components of L layer (undecomposed, identifiable material) and in panel B the sum of identifiable components, F layer (fragments, unidentifiable matter), sum L + F, litter+ (that was not separated into L and F), and total litter (all standing litter observations). "*n*" indicates the number of observations. The bars represent median and the vertical lines the 25th and 75th percentile, respectively.

including duff but excluding humus; see Methods). Our definition of SL excludes CWD (>2.6 cm diameter) and dead grass/understory, which have been quantified by a number of studies, adding substantially to carbon pools as well as fuel loads (see Appendix S1: Fig. S4). For CWD and grass pools, there are few data (i.e., fall of material >2.6 cm diameter; mortality of grass and herbaceous understory, Appendix S1: Fig. S5). Reported CWD can be at least equal to or greater than SL.

SL (leaves, twigs <2.6 cm diameter, bark) accumulates slowly with time since fire (TSF) > five years, our threshold for calculating LD constants (k) (Appendix S1: Fig. S3). Values of k were more variable than either SL or LF. The median value of $k \pm 50\%$ of interquartile range was 0.396 ± 0.518 yr^{-1} to accommodate skewness (mean and standard deviation is 0.663 ± 0.707 yr^{-1}). Variance in k is thus typically 90% of the mean (compared to variances of 50% for LF and 85% for SL). Eucalypts had smaller k (slower decomposition) than rainforest species (Appendix S1: Fig. S7). We note large variation of k within species groups with some *Eucalyptus* spp. having greater k and some rainforest species smaller k. *Pinus radiata* and *P. elliottii*—two widely planted commercial non-native conifers in Australia—had k 0.294 ± 0.302 yr^{-1} (median and interquartile range). More simply, rates of decomposition for these conifers are slightly slower relative to eucalypts (0.341 ± 0.237 yr^{-1}). Species associated with nitrogen-fixing symbiotic bacteria like *Acacia*, *Casuarina,* or *Allocasuarina* spp. also displayed large variation in k (Appendix S1: Fig. S7).

Variation in litter composition

Pooled twig and bark material contributed ~38% to LF but 60% to SL (Fig. 3) due to slower decomposition of woody litter. Twig and bark k ranged between 0.007 and 2.268 yr^{-1} for eucalypts, while the range for leaf k was between 0.107 and 7.305 yr^{-1} (Fig. S8). Varying LD and the composition of LF (e.g., leaves vs. twigs) drive SL (Appendix S1: Fig. S8). Species identity explained only a small portion of this variation (Appendix S1: Fig. S7).

We found 49 instances in 12 studies (Appendix S1: Table S3) where LF and SL assessments included both leaves and twigs on sites unburnt for at least five years. For these studies, we compared the proportions of leaves and wood (twigs and bark) in LF and SL. This analysis reveals that under long unburnt conditions, SL differs strongly from LF. Leaves dominated LF, but twigs represented more than half of SL (Fig. 4A). Separating these high-quality studies by climate revealed declining proportions of leaves in SL and increasing proportions of twigs under wet conditions in south-east and coastal regions (Fig. 4B, C; Appendix S1: Fig. S10). Under seasonal climates (mostly in Western Australia, Southern Australia and inland New South Wales and Queensland), shares of leaves and twigs to LF and SL were similar. The available data for coarse woody debris (CWD) >2.6 cm support the pattern of declining k as material becomes more lignified (leaves 1.080 yr^{-1}, twigs 0.424 yr^{-1}, CWD 0.113 yr^{-1}; Appendix S1: Fig. S11).

Drivers of litterfall and litter decomposition

Precipitation was most strongly related to leaf LF and explained 26% of variation (Appendix S1: Table S4). Wood LF was less well related to single climate variables and precipitation only explained a small proportion of the variance (R^2 = 0.029). TSF (R^2 = 0.049) and soil carbon

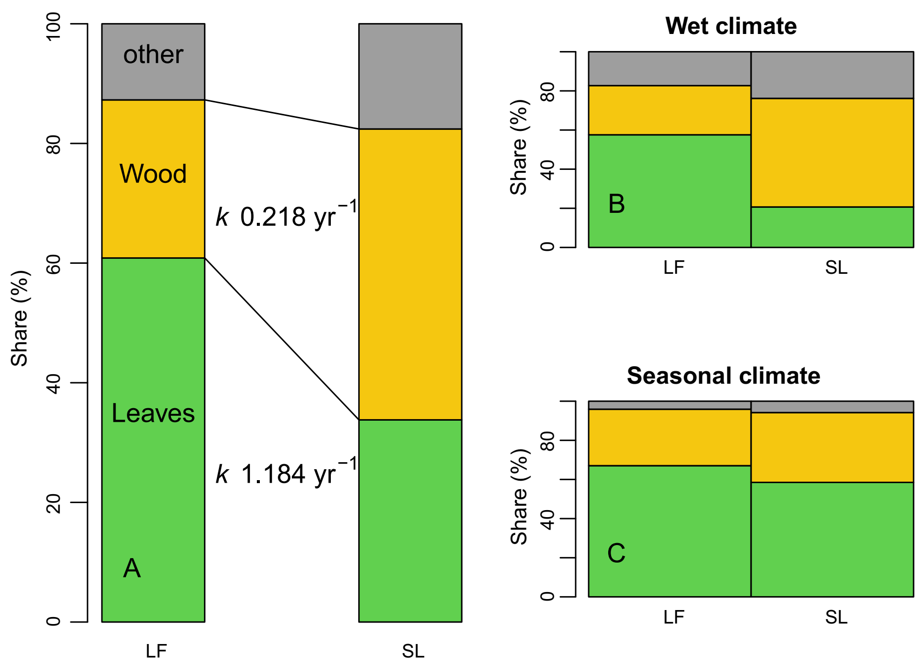

Fig. 4. Share of leaves, wood (twigs, bark), and other material in litterfall (LF) and standing litter (SL) for studies that were unburnt and separated LF and SL into components (n = 49) in panel A. Average decomposition constants (k) are shown for leaves and wood. We split the data into "wet climates" (warm wet, hot wet, and cool wet) in panel B (k leaf 1.717 yr^{-1}, k wood 0.219 yr^{-1}) and "seasonal climates" (warm seasonal and hot seasonal) in panel C (k leaf 0.472 yr^{-1}, k wood 0.273 yr^{-1}). There are no suitable studies in cold, arid, and semiarid climates.

($R^2 = 0.042$) provided similarly weak predictive power. None of the single potential drivers of LD (e.g., precipitation, longitude, TSF, measurement year, stand age) had strong influence (Appendix S1: Table S4).

We further evaluated potential models of LF using precipitation as a covariate. Precipitation accounted for much of the variation in leaf LF across its full range (Fig. 5A). Most observations were from sites with rainfall of 400 to 1700 mm/yr, and both leaf and wood LF varied similarly with precipitation (Fig. 5AB). Fig. 5C,D shows that LD is less well correlated with precipitation than LF. Based on residual variation, leaf LF for all species groups can be represented with comparable bias by linear models based on precipitation (Appendix S1: Fig. S9).

Some studies measured LF over more than one year, and we explored annual variation in LF in more detail in an attempt to reconcile unexplained variances (Fig. 5; Appendix S1: Table S4). Both leaf and wood LF showed large ranges (i.e., inter-annual variation) across all climates and species and from low to high LF (Appendix S1: Fig. S2). LF varied on average by 25% between years and many sites displayed a range in variation of up to 100%.

No single climate variable provided strong explanatory power in multiple linear models of SL. Fire history and stand structure account for some of the variation (Appendix S1: Table S5)

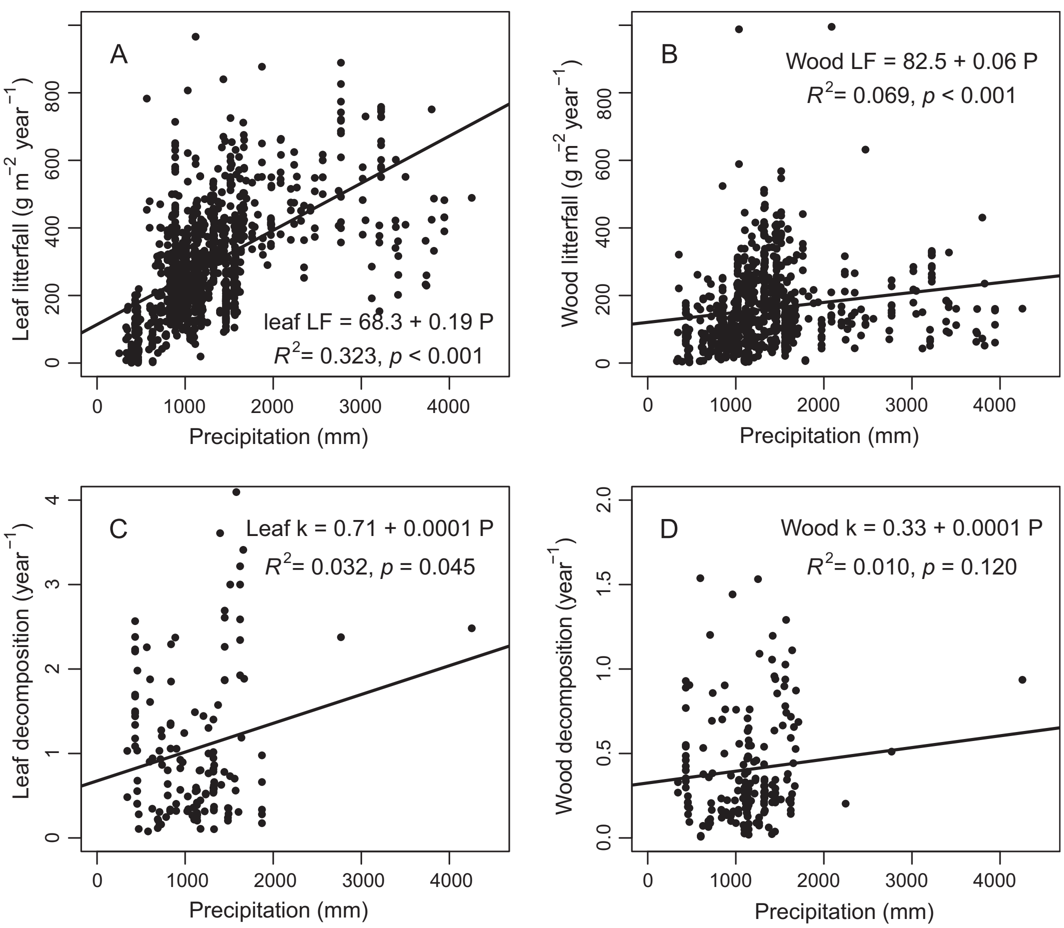

Fig. 5. Simple linear models based on precipitation for leaf litterfall (A), wood (twigs, bark) litterfall (B), leaf decomposition (C), and wood decomposition (D). We show functions, coefficients of determination (R^2), and P values of regression (see also Appendix S1: Table S4).

confirming Objective 2. Together, TSF, stand age, and basal area explained most variation (with R^2 ranging from 0.14 for woody SL to 0.22 for L + F), while R^2 for single covariates are about 0.04–0.18 (Appendix S1: Tables S5, S6). SL increased with increasing TSF for all litter components and litter layers. Non-linear effects of stand age (second-degree polynomial) were observed for SL in the L and L + F layer (Appendix S1: Table S5). Basal area was positively correlated to all components of SL in a linear fashion.

Discussion

This comprehensive database for necromass (n litterfall = 1825, n standing litter = 3914, n litter decomposition = 629) can now be used for studying nutrient cycling, carbon storage, or fuel accumulation. We focus the following discussion on (1) data quality, (2) mechanisms of litter decomposition, (3) drivers of litterfall and decomposition in Australia (known for highly variable climate, drought, and fire), (4) contrasting litter dynamics in Australian ecosystems with respect to other ecosystems worldwide, and (5) implication of our study for upscaling observations to the landscape.

Consistency of data

Leaf LF and leaf SL are the most straightforward additions and standing pools of necromass in forests. Measurements of both are generally reliable. However, measurements of woody components are far less reliable, often depending on the purpose of measurement. SL is most frequently classified according to its dimensions. Hence, coarse woody debris is most often defined as having a minimum diameter of 2.5 cm (or 2.6 cm allowing for conversion between imperial and metric systems; Woldendorp and Keenan 2005). We adopted this definition. Fuel studies sometimes further separate woody material into 0–0.6 cm (fine fuel) and 0.6–2.6 cm (coarse fuel). The reasoning behind such separation is related to the time taken for complete combustion (negligible for leaves and 0–0.6 cm twigs; 1 h for 0.6–2.6 cm material; Gould and Cruz 2012, Keane 2015). We used a limit of 2.6 cm in order to reduce inconsistency among Australian studies. All studies included twigs up to a diameter of 0.6 cm and in most cases up to 2–2.6 cm. In contrast to Watson (2012) who adjusted data to a common basis of 0–0.6 cm for "twigs," we made no such adjustment. As a simple check, we re-analyzed data from a range of eucalypt forests (see Appendix S1: Table S5 for references). The ratio of twig mass (0.6–2.6 cm) to that <2.6 cm, ranges from 0.109 to 0.203 (average 14.3%; Appendix S1: Table S7). In other words, for a hypothetical 1000 g/m^2 of standing litter, the error introduced by excluding the 0.6–2.6 cm twigs, amounts to reducing the reported SL to ˜860 g/m^2. If LF was 500 g·m^{-2}·yr^{-1}, then k would be overestimated by 14% (if LF would include 0–2.6 cm twigs). Our reported SL and k (Figs. 2, 5; Appendix S1: Table S1) are thus underestimates of SL and overestimates of k, by ˜10–15% in the worst case, assuming that all studies excluded 0.6–2.6 cm twigs. 20% of our SL data excluded 0.6-2.6 cm twigs and 7% excluded 1–2.6 cm twigs, based on information on sampling provided in the references. Our underestimation then falls to ˜3%.

Mechanism of litter decomposition

Data reported here for LF and SL at 629 sites × years across Australia provide a first continental analysis of LD (e.g., decomposition constants k, based on Olson's mass balance) for the southern hemisphere. We note also the lack a "southern synthesis" of decomposition based on litter bags (Krishna and Mohan 2017), in comparison to the heavily scrutinized litter bag data from the northern hemisphere (e.g., Zhang et al. 2008, Prescott 2010, Bradford et al. 2014).

Olson's theoretical approach to LD (correctly attributed to Jenny et al. [1949]) was principally designed to capture and represent environmental conditions at very large (global) spatial scales. The utility of Olson's k depends on the assumption of steady state or quasi-equilibrium and invariable inputs (Olson 1963, Turner and Lambert 2002). While Olson presented approaches to capture temporally variable inputs of LF—which can significantly affect SL—the underlying model and quantification of k retained the steady-state assumption. Olson's k reported here (median ± interquartile range = 0.357 ± 0.308 yr^{-1}, minimum = 0.035 yr^{-1}, maximum = 2.998 yr^{-1}) is based on all published data fulfilling our quality criteria (weighed destructive samples, comparable definition of SL and LF, unburnt). Across the Australian continent, and assuming the SL attains an equilibrium mass (a questionable assumption, see Birk and Simpson 1980), Olson's k suggests it takes an average of ˜2.8 yr for material <2.6 cm to decompose. We compare our data with international literature below in *Litter decomposition in Australian forests vs. other global ecosystems*.

Decomposition constants can also be derived using a range of other methods (e.g., litter bags, in situ studies). However, all studies show large differences in rates of decomposition between leaf and non-leaf material. While non-leaf material only represents about one third of total LF, twig, and bark material accumulate much more strongly with time as the litter layer becomes more complex and more variable, in particular for bark-shedding eucalypts (O'Connell 1987). An important conclusion is that sampling and analysis regimes, especially those designed for fuels, must be modified to properly account for non-leaf components. Even more problematic is the assumption of steady state (see Gould and Cruz 2012) that underpins use of Olson's k. A very high proportion of the Australian sclerophyll forest estate is subject to fire, albeit at widely varying intervals. TSF is a determinant of LF and LD, and a highly variable determinant of SL. In contrast to much of the forests of Europe and the non-fire-prone parts of North America where steady-state assumptions are reasonable, they are seldom appropriate for many, if not most, Australian ecosystems or other fire-prone regions (e.g., Mediterranean Basin, California, Southern Africa).

Drivers of LF and SL

Our LF data (n = 1825) confirm the broad importance of climate (Vitousek 1984, Liu et al. 2004, Neumann et al. 2018). In Australia, all tree species (including native conifers *Callitris* spp. or *Araucaria* spp., nitrogen-fixing *Acacia* spp., close relatives of eucalypts like *Melaleuca* spp. and also introduced *Pinus*) produce more LF under warm and moist conditions—a feature previously reported for *Eucalyptus* spp. and rainforests (Adams and Attiwill 1991).

Potential evapotranspiration (PET) mostly exceeds precipitation in Australian ecosystems. Only in the wet tropics, some coastal regions, and parts of Tasmania, is PET routinely less than precipitation. In broad terms, precipitation had the strongest explanatory power for leaf LF, followed by evapotranspiration. As shown in Fig. 5 A, the relationship between leaf LF and precipitation is non-linear, with a peak at ˜2000 mm. A similar pattern was noted in a Eurasian study (Liu et al. 2004). Relations among temperature, precipitation, and tree growth are equally unlikely to be linear.

We expected that SL would reflect the same drivers as LF, assuming that rates of accumulation of SL should be related to inputs. However, SL was not well correlated with climate variables (Appendix S1: Tables S5–S6). Among climate variables, maximum temperature had the strongest effect (R^2 = 0.128). On average, unburnt sites had >1000 g/m^2 greater SL than recently burnt sites (Appendix S1: Fig. S12). LD clearly ranks alongside LF as the contributors to SL. A recent study in subtropical eucalypts showed that LD was invariant to LF (Wang et al. 2019), and we can find no studies that suggest inputs of LF is a major control of LD. Instead, litter quality, solar radiation, and biological processes—including the full complex suite of decomposer organisms—have dominant roles in litter decomposition (Austin and Vivanco 2006, Prescott 2010, Bradford et al. 2014).

Forest structure (i.e., tree density, stand age) helps explain temporal and spatial patterns in LF in European forests (Neumann et al. 2018), but has only rarely been considered in Australia (Turner and Lambert 2002). Data reported here show that stand age had a positive effect on non-leaf LF. For leaf LF and LD, basal area and stand age had poor explanatory power compared to climate in single linear models. SL increases with basal area, but decreases with increasing age (Appendix S1: Table S5). Wide spacing between mature trees may increase exposure of litter to sunlight and promote litter decomposition through photodegradation, that appears to be important across ecosystems (Austin and Vivanco 2006, Marinho et al. 2020). We acknowledge uncertainties in attributing a single age to entire stands, as well as stand-replacing fires in some forest types, makes it difficult to derive conclusive results as to the effect of tree age on litterfall (Ashton and Martin 1996). We note that single-variable LF and SL models are not able to attain high explanatory power, while models considering interactions between stand, fire history, and climate and the litter components separately appear more promising.

Litter decomposition in Australian forests vs other global ecosystems

Data access limits the value of some global datasets (Shen et al. 2019). Methodological inconsistencies further weaken the basis for testing generic or continental differences in SL and LD. In a global dataset covering 1827 until 1997 (Holland et al. 2015), there are few sites (n = 23) with both LF and SL data measured on the same site. These 23 sites produce a wide range of Olson's k, from 0.005 to 8.449 yr^{-1}. More recently published or recalculated k range from 0.843 to 1.070 yr^{-1} for tropical dry forests in Mexico (Anaya et al. 2012) and 0.166 yr^{-1} for *Pinus taeda* plantations in southeast United States (Binkley 2002). For Indian subtropical forests, k ranged from 0.459 to 1.701 yr^{-1} (Rout and Gupta 1990*a*, *b*, not reported in Holland et al. 2015). For European temperate forests, k was determined to be 0.066 to 1.088 yr^{-1} (Vesterdal and Raulund-Rasmussen 1998, Hansen et al. 2009), while for boreal forests k ranged from 0.050 to 0.106 yr^{-1} (Kleja et al. 2008).

Our results, as well as those from a global meta-analysis of litterbag studies (Zhang et al. 2008), show that rates of decomposition vary strongly with the nature of the material decomposing. Separating leaf from non-leaf material is essential to understanding decomposition. For example, average Olson's k for total litter across Australia was 0.498 ± 0.435 yr^{-1} (mean ± SD), while that for leaf litter alone was 1.093 ± 0.997 yr^{-1}. Olson's k for Australian litter is considerably less than global broadleaf (0.73 yr^{-1}) and mixed forests (0.55 yr^{-1}), but similar to conifer forests (0.35 yr^{-1}). Two widely planted introduced conifers in Australia (*Pinus radiata* and *P. elliottii*) have average k of 0.396 yr^{-1} (range from 0.103 to 2.000), or roughly the same as reported for conifers globally (Zhang et al. 2008). Litter decomposition in pine plantations in Australia is generally slower than in native eucalypt forests, perhaps due to nutrient and water limitations (Paul and Polglase 2004). While eucalypt litter is poor in nutrients and slower to decompose than other native species (Cizungu et al. 2014), it more quickly decomposes than litter of introduced tree species under the same conditions of climate and soil.

At the global scale, decomposition (of both leaves and wood) increases with temperature and precipitation (Zhang et al. 2008). At smaller scales, the picture is more nuanced. For continental United States, warmer conditions favor slower foliage and twig decomposition while precipitation had no clear effect (Keane 2008). In the Rocky Mountains, foliage decomposition ranged from 0.085 to 0.283 yr^{-1} while that of woody fuels ranged from 0.045 to 0.125 yr^{-1}. In other states of western United States, and in Canada, decomposition rates for foliage ranged from 0.005 to 0.56 yr^{-1}, for twigs from 0.005 to 0.24 yr^{-1} and for larger logs from 0.001 to 0.115 yr^{-1} (Keane 2008).

Simple linear models are not able to explain the complex interactions of climate, litter quality, litter input, and biotic decomposers (Prescott 2010, Bradford et al. 2014, 2016). Bradford et al. (2016) used a consistent dataset (standardized litterbags with needles of *Pinus sylvestris*) and reported non-linear relationships between decomposition and temperature, supporting literature from North America and our study. In cold climates (below 5°C mean annual temperature, MAT), there was a clear positive temperature response of decomposition, up to about 7°C. Between 7 and 15°C—the greatest MAT in the Bradford et al. (2016) dataset—further increases in temperature resulted in little change in decomposition. Our data for Australian ecosystems span a MAT range of 6.5–27.4°C. Our data again show a weak response between 7° and 15°C (Fig. 6). However, between 15° and 27°C rates of decomposition again show a clear temperature effect (R^2 = 0.21, Fig 6). The temperature response of leaf/needle decomposition also applies to non-leaf litter (Fig. 6). In summary, decomposition in Australia as well as in northern hemisphere ecosystems responds to temperature in a complex manner.

Implications of results at the landscape scale

Combining a zonal classification (Figs. 1, 2; Appendix S1: Table S2) with land cover maps allows straightforward upscaling of LF and SL. Models of LF will benefit from current developments to map climate (precipitation or evapotranspiration) at greater resolution. A simple

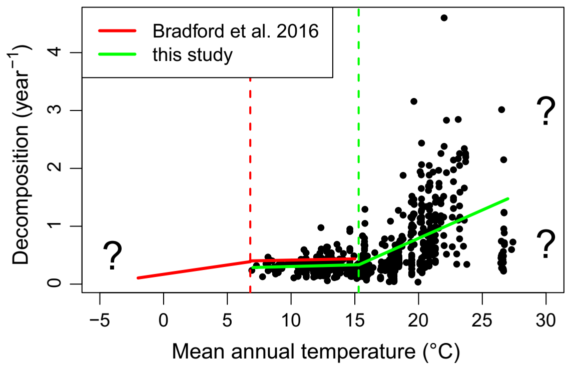

Fig. 6. Temperature response on decomposition. Solid lines are the linear trend functions, in red from Bradford et al. (2016) after transforming mass loss to decomposition constants and in green based on this study. The dashed vertical lines indicate breakpoints, where slopes of linear regressions become non-significant. Using segmented regression with the observations of this study, we derived a breakpoint at 15.3°C. Question marks indicate temperatures, not covered by this study or Bradford et al. (2016).

linear model based on average annual precipitation captures about one third of the observed variation in LF (Appendix S1: Table S4). This is remarkable considering large annual variation in LF (average variation of 25%; maximum variation of 100%; Appendix S1: Fig. S2). Unexplained variation is likely due to local topographic/soil variation, as well as variation in stand structure (age-related) and climate seasonality/anomalies. Further analysis of seasonal and/or annual climate covariates or using stand structure as covariate may thus help reduce unexplained variance.

TSF is obviously a major issue for estimating SL in Australia (Appendix S1: Table S5–S6). Models of fuel load rely on the existence of a clear TSF relationship (Tolhurst et al. 2008). Increasing availability of spatially explicit data for fire history (Attiwill and Adams 2013) can be combined with field observations to produce maps at the landscape scale (Eastaugh and Vacik 2012). We caution against using TSF as a sole predictive variable for fuel loads alongside assumptions of steady state (Watson 2012, Roxburgh et al. 2015). Such approaches lead to unrealistic results. Undetected fires, variable fuel consumption, lack of calibration for specific vegetation types, and non-linear relationships of LD with climate all contribute to a non-equilibrium condition. Further research into spatial and temporal patterns of LF and LD are needed to develop process-based models of SL that are widely applicable and robust. We support the suggestion made by Gould et al. that non-asymptotic models of SL (e.g., SL = (a × age)/(b + age)) are essential (Gould et al. 2011).

Necromass contains dynamic and highly variable pools of carbon, energy, and nutrients. Turnover of necromass is frequently large and spatial and temporal variations in LF and LD heavily constrain regional and global carbon models. For example, average NPP across Australia woody ecosystems is ~1147 g C·m^{-2}·yr^{-1} (based on remote sensing, Zhao and Running 2010). Our data show that on average, LF amounts to 468 g·m^{-2}·yr^{-1} or roughly 234 g C·m^{-2}·yr^{-1} or ~20% of NPP. Similarly, the average SL of 1107 g/m^2 is equivalent to about two years of LF. Our compiled data for the Australian continent complements assessments for tropical forests (Malhi et al. 2011), for Eurasian forests (Liu et al. 2004), and for Europe (Neumann et al. 2018). Such assessments of LF, LD, and SL are essential to understanding anomalies in regional and global C cycles (Poulter et al. 2014).

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Data Availability

The data used in the analysis are available from Figshare: https://figshare.com/articles/dataset/Litterfall_and_standing_litter_of_Australian_woody_ecosystems/13160351.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3693/full