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Tansley review: are litter decomposition and fire linked through plant species traits?

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Citation

Cornelissen, J. H. C., Grootemaat, S., Verheijen, L. M., Cornwell, W. K., Bodegom, P. M. van, Wal, R. van der, & Aerts, R. (2017). Tansley review: are litter decomposition and fire linked through plant species traits? *New Phytologist*, 216(3), 653-669.
doi:10.1111/nph.14766

Version: Publisher's Version
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Downloaded from: <https://hdl.handle.net/1887/3201988>

Note: To cite this publication please use the final published version (if applicable).



Tansley review

Are litter decomposition and fire linked through plant species traits?

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Received: 26 April 2017
Accepted: 19 July 2017

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Summary

New Phytologist (2017) **216**: 653–669
doi: 10.1111/nph.14766

Key words: biogeochemical cycling, decomposition, fire ecology, flammability, leaf litter quality, nonadditivity, plant functional traits, woody debris.

Biological decomposition and wildfire are connected carbon release pathways for dead plant material: slower litter decomposition leads to fuel accumulation. Are decomposition and surface fires also connected through plant community composition, via the species' traits? Our central concept involves two axes of trait variation related to decomposition and fire. The 'plant economics spectrum' (PES) links biochemistry traits to the litter decomposability of different fine organs. The 'size and shape spectrum' (SSS) includes litter particle size and shape and their consequent effect on fuel bed structure, ventilation and flammability. Our literature synthesis revealed that PES-driven decomposability is largely decoupled from predominantly SSS-driven surface litter flammability across species; this finding needs empirical testing in various environmental settings. Under certain conditions, carbon release will be dominated by decomposition, while under other conditions litter fuel will accumulate and fire may dominate carbon release. Ecosystem-level feedbacks between decomposition and fire, for example via litter amounts, litter decomposition stage, community-level biotic interactions and altered environment, will influence the trait-driven effects on decomposition and fire. Yet, our conceptual framework, explicitly comparing the effects of two plant trait spectra on litter decomposition vs fire, provides a promising new research direction for better understanding and predicting Earth surface carbon dynamics.

I. Introduction

The flux of biogenic carbon (C) back to the atmosphere is a critical control on global atmospheric CO₂ (and CH₄) concentrations and, thereby, the global climate (Sitch *et al.*, 2003; IPCC, 2013). Conversions of organic matter in terrestrial plants, in both living and dead parts, play a key role in this controlling function (Gorham, 1991; Bonan, 2008; Pan *et al.*, 2011). Besides autotrophic respiration and herbivory, decomposition and fire are the two predominant processes that mineralise organic C and return it to the atmosphere in inorganic form. Whilst microbial decomposition (whether or not promoted by fauna via herbivory or fragmentation) drives relatively slow release of C from dead plant material, fire causes fast, episodic C release through combustion (Cornwell *et al.*, 2009; Hyde *et al.*, 2011). Because these two pathways differ greatly in both the frequency and the speed at which CO₂ is released, and because they compete for the same substrate, the rate of C release from the Earth's land surface may change considerably if and where the prevalence of either pathway shifts substantially.

Decomposition and fire have generally been studied separately, even though they are clearly not independent (Fig. 1; Brovkin *et al.*, 2012; Hyde *et al.*, 2011). For instance, under adverse (e.g. cold or dry) environmental conditions and poor litter quality, slow litter decomposition leads to organic matter accumulation, which creates a growing pool of fuel 'waiting' to go up in flames (Dos Santos & Nelson, 2013). Also, the decomposition stage of plant litter or coarse woody debris, through the reduction of tissue density, can be a strong determinant of its flammability (Hyde *et al.*, 2012; Zhao *et al.*, 2014). In the other direction, fire will combust dead organic matter either completely and thereby reduce the availability of substrate for microbial decomposition, or incompletely (e.g. by charring), and thereby decrease its decomposability (Preston & Schmidt, 2006; Hart & Luckai, 2013; Marañón-Jimenez & Castro, 2013); however, char can also have important indirect positive effects on microbial decomposition and soil fertility (Atkinson *et al.*, 2010; Biederman & Harpole, 2013). Finally, fire can also kill or alter decomposer communities, thereby indirectly altering the decomposition of remaining or newly produced litter (Neary *et al.*, 1999). The predominance and rates of these two pathways of C release in different biomes, now and in the future, depend on abiotic and biotic drivers and their interactions. Moisture and temperature regimes are well-studied direct abiotic controls on both decomposition (Swift *et al.*, 1979; Harmon *et al.*, 1986; Cornelissen *et al.*, 2007b; Chapin *et al.*, 2011) and fire (Rothermel, 1972; Bond & Van Wilgen, 1996; Bowman *et al.*, 2009; Chapin *et al.*, 2011; Keeley *et al.*, 2012; Matthews *et al.*, 2012; Varner *et al.*, 2015). We also acknowledge that litter surface fires, even when fuel availability is sufficient, can be limited by ignition sources and frequencies in some systems (Macias-Fauria *et al.*, 2011).

Here we will concentrate on biotic factors, especially litter traits, as determinants of the balance between the decomposition and fire pathways, which remains poorly understood (Chapin, 2003; Cornwell *et al.*, 2009). We focus on decomposition vs combustion

of dead plant material (leaf and fine wood litter, coarse woody debris) on the soil surface. While we do stress the important contributions of standing live (Bond & Midgley, 1995; Albin *et al.*, 2012; Pausas, 2015) and dead biomass (Grigulis *et al.*, 2005; Cornwell *et al.*, 2009) and soil organic matter (Mack *et al.*, 2011) to both processes, we consider the litter layer particularly important for a wildfire to start and to spread laterally (Plucinski & Anderson, 2008; Dos Santos & Nelson, 2013), or vertically, thereby starting smouldering fires in organic soils or crown fires via fuel ladders (Blauw *et al.*, 2017). Moreover, the litter layer is where the interactions between decomposition and fire are probably the most important. We will specifically evaluate how spectra of trait variation among living plants impose afterlife effects of these traits on the rates and pathways through which C returns to the atmosphere.

The species composition of a given plant community is important for decomposition and fire regimes in two complementary ways. First, it determines the depth of the litter layer via vegetation dimensions, structure and productivity (see Fig. 1). Second, and central to this review, the species composition of vegetation is a strong determinant of the properties of the surface litter layer. This is because the functional traits of the living stems and leaves of different component species tend to impose strong afterlife effects, via senescence, on litter quality (Cornelissen, 1996; Cornwell *et al.*, 2008; Freschet *et al.*, 2012a; Ganteaume *et al.*, 2013; Pietsch *et al.*, 2014). Here we ask the critical question whether the afterlife effects of trait variation on litter properties have corresponding consequences for decomposition rates and flammability variables across species. All else being equal, if the same plant traits promote (or inhibit) decomposition and fire in a consistent manner across species, then decomposable litter should generally be flammable while fire-retardant litter should generally be recalcitrant to microbial decomposition. This could then lead to a divergence of, on the one hand, fast litter turnover and low surface C storage in ecosystems dominated by species that produce highly decomposable and flammable litter and, on the other, litter and C accumulation in ecosystems dominated by species that produce recalcitrant, poorly decomposable and less flammable litter. However, apart from two recent empirical studies on this theme (Grootemaat *et al.*, 2015, 2017a) we are not aware of any other study that has explicitly considered linkage between trait effects on flammability and trait effects on decomposability. Here we synthesise the literature that addresses components of this potential connection through our new conceptual framework (Fig. 2). This framework contains two key building blocks, namely the plant economics spectrum (PES) and the size and shape spectrum (SSS):

(1) The species effect on litter decomposition rates should be closely linked to afterlife effects of traits that are critical to the nutrient and C economy of plant organs (Cornwell *et al.*, 2008; Freschet *et al.*, 2012a; Pietsch *et al.*, 2014; Reich, 2014). These traits have been integrated into the 'leaf economics spectrum' (Wright *et al.*, 2004) and, with inclusion of other fine organs, into the PES (*sensu* Freschet *et al.*, 2010).

(2) While we acknowledge the importance of chemical traits and internal tissue density as contributors to flammability (e.g. Ormeno

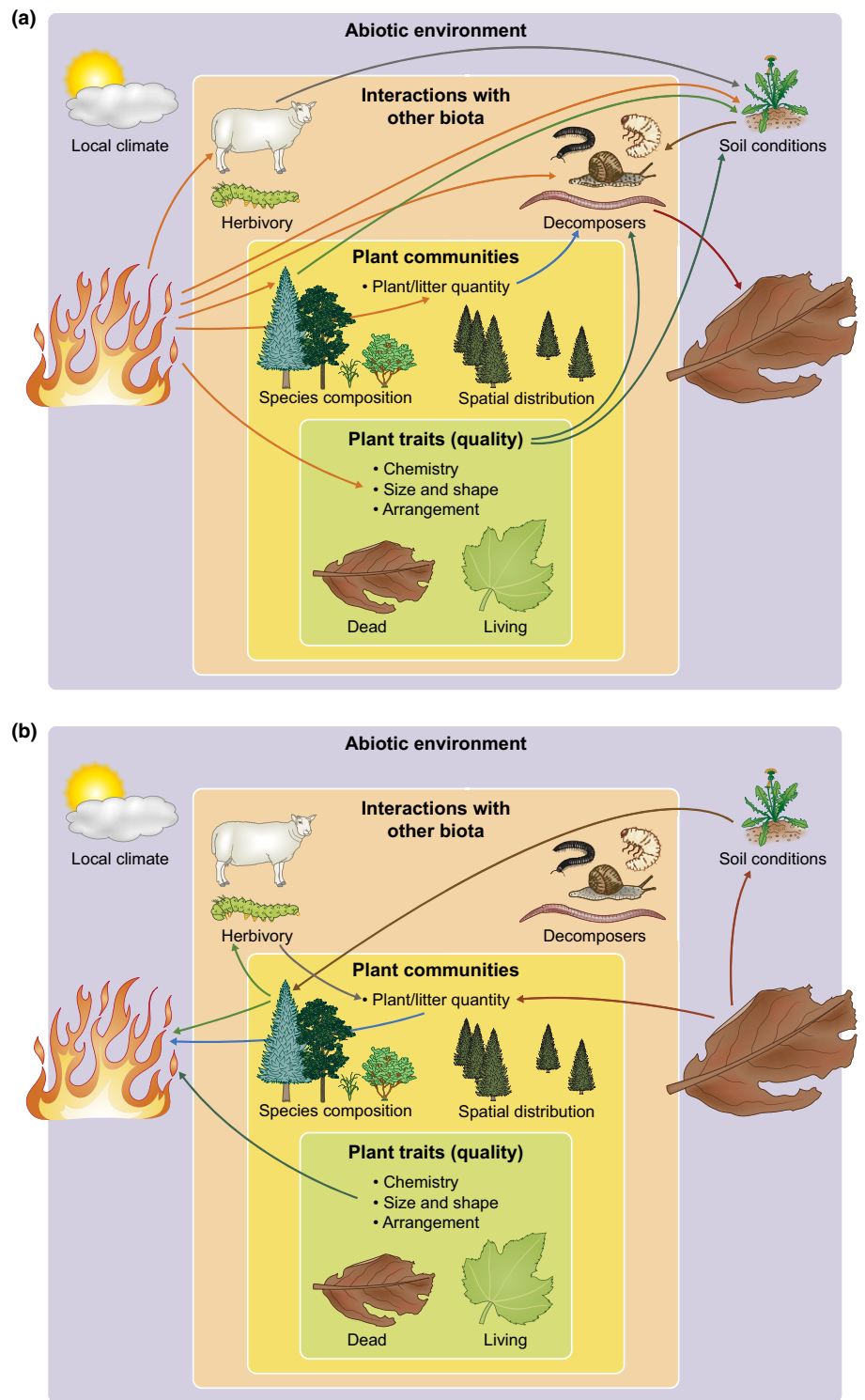


Fig. 1 Fire–decomposition feedbacks with a central role for plant traits of different species, adding concentric shells of real-world complexity through community-level interactions and other biotic and abiotic drivers. For clarity the two directions of these feedbacks are separated here: (a) fire effects on decomposition and (b) decomposition effects on fire. The core represents the role of plant traits; the shell around it represents ecosystem-level factors such as community composition and species (litter) interactions, and amount and spatial configuration of vegetation and litter (fuel). The next shell adds other biotic interactions while the outer shell represents the (local to global) abiotic drivers that may affect processes and connections within the inner shells.

et al., 2009; Zhao *et al.*, 2014; Varner *et al.*, 2015), the species effect on litter combustibility should be strongly controlled by oxygen availability through the sizes and shapes of litter particles of different species (cf. Scarff & Westoby, 2006; Schwilk & Caprio, 2011; Engber & Varner, 2012; Cornwell *et al.*, 2015; Varner *et al.*, 2015; Belcher, 2016; Grootemaat *et al.*, 2017b), in particular the sizes and shapes in which they are shed from the plant to join the surface litter horizon. Here we refer to interspecific variation in such

traits as the SSS (see Dias *et al.*, 2017). Flammability is a broad term that comprises several aspects of fire behaviour (Anderson, 1970; see Box 1), including ignitability, combustibility, fire sustainability and fire severity. We will distinguish explicitly between these different parameters, as they may be driven by different plant traits.

When highlighting the extremes of the trait gradients for conceptualisation, there are four theoretical main scenarios by which the trait combinations of different species may affect the

Box 1 Glossary of terms**Fire-related terms**

Combustibility: how well something burns (e.g. rate of fire spread, fire intensity).

Flammability: umbrella term used to describe the potential for a material to burn; capturing various terms (e.g. ignitability, combustibility, fire sustainability) representing different stages of fire development.

Fire intensity: term describing the physical combustion process of energy release during a fire; can be described as combinations of different fire measurements (e.g. maximum temperature, energy release in kW m^{-1} , flame size).

Fire severity: the effect that a fire has on an ecosystem, one aspect of which may be the percentage of potential fuel consumed (i.e. consumability).

Fire sustainability: length of burning time (including both flame and smouldering phase).

Ignitability: ease of ignition, that is the energy needed for the onset of a fire (flame appearance, heat production) or (inversely) the time until ignition at a given energy supply.

Smouldering: flameless, often incomplete combustion on the surface of a fuel in the solid phase.

Decomposability

The rate of decomposition of a material relative to that of other materials (e.g. litter type or species) when compared with similar methodology, simultaneously, in a similar environment.

pathway and rate of C return to the atmosphere (Fig. 2): high vs low decomposability combined with high vs low flammability. Building on this framework we ask our central question: *is the variation among species in their leaf and stem resource economic strategy (PES) largely decoupled from the size and shape of their leaves and stems (SSS)? Such decoupling of trait spectra among living species would*

mean that the carbon turnover processes they influence would also be decoupled if PES-related traits indeed primarily drive decomposition and (different) SSS-related traits primarily drive fire behaviour in surface litter. In that case, all four theoretical combinations, and their intermediates, could exist on Earth (Fig. 2). In the case of both strong coupling and strong decoupling the C emission

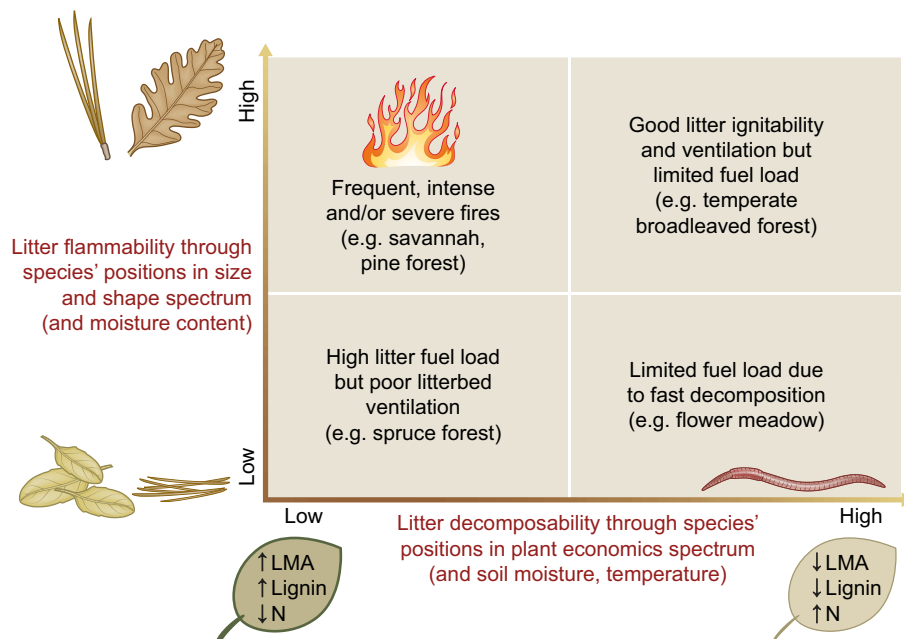


Fig. 2 Conceptual diagram showing possible relationships between surface litter flammability and decomposability in a highly simplified way by defining four broad categories of low vs high decomposability and flammability. (Intermediates between these categories do occur but have not been shown here.) This concept can serve as a starting point for understanding the role of plant traits in the fates and rates of surface litter from individual plants to ecosystem scale in different biomes. The concept adopts the hypothesis that fire regimes (*sensu* Morgan *et al.*, 2001) with higher frequency, intensity and/or severity are only possible in vegetation where the plant-trait composition of the predominant species has both inhibitory effects on decomposition of their litter (moderated by soil moisture and temperature; see x-axis label) and fire-promoting effects given the occurrence of drought periods (via litter moisture content; see y-axis label). Litter trait states are indicated by cartoons along the axes: LMA, leaf mass per area; N, leaf nitrogen concentration. Note that the positive effect of N on decomposition is generally measured during early decomposition whereas it can be negative during later stages. In the lower left quadrant, systems with poor surface litter ventilation and flammability, and low decomposability, may still be susceptible to a major fire during extreme drought combined with strong wind.

consequences of functional shifts in vegetation composition would be predictable, whereas partial coupling would lower such predictive power. Litter flammability depends on a combination of direct climatic effects on decomposition and trait-driven feedbacks (see Figs 1, 2, and the section VI 'Feedbacks between community (trait) composition, decomposition and fire'). Only in ecosystems where traits and climate together inhibit litter decomposition leading to strong fuel accumulation, and where high SSS rankings will promote litter flammability during drought periods, will fire regimes (*sensu* Morgan *et al.*, 2001) with higher frequency, intensity and/or severity be able to prevail in the longer term (Fig. 2, top left quadrant). While this hypothetical framework is highly simplified and ignores intermediate scenarios as well as other important factors and interactions that also influence both decomposition and fire (Fig. 1), it should help as a conceptual starting point from which we can work up to real-world complexity.

Below we synthesise the literature to answer our central question drawing on examples from contrasting biomes and ecosystems. We first introduce the main traits underpinning the PES and SSS as well as their connections with decomposition and fire at the plant to small plot (i.e. plant community) scale (Fig. 1). We then combine these two lines of plant effects on C release for single species in given environments. Subsequently, we discuss possible contributions of community-scale properties and interactions to the PES–decomposition vs SSS–fire relationships. Finally, we briefly discuss how long-term feedbacks through species turnover and changes in soil and vegetation properties may play out in the context of our framework and influence surface C dynamics in different biomes.

This paper offers, to our knowledge, the first conceptual perspective to explicitly discuss whether, and if so how, fire and decomposition may interact through the functional trait composition of the vegetation and especially of the litter it produces. Such an understanding will aid in developing the next generation of dynamic vegetation models that incorporate feedbacks from vegetation functional trait composition into regional and global predictions of C stocks and climate (see Brovkin *et al.*, 2012; Van Bodegom *et al.*, 2012; Baudena *et al.*, 2015).

II. Decomposition–fire interactions via traits in the plant economics spectrum (PES)

Current theory posits that fundamental trade-offs related to the investment of finite resource pools of C, nitrogen (N), phosphorus (P) and other resources create covariation in growth and reproductive traits; furthermore, the position of a given individual plant along these axes of variation indicates its ecological strategy (Reich *et al.*, 1997; Aerts & Chapin, 2000; Grime, 2001; Westoby *et al.*, 2002; Fortunel *et al.*, 2012; Reich, 2014; Díaz *et al.*, 2016). One well-known set of correlated traits defines the 'leaf economics spectrum' (LES, Wright *et al.*, 2004). Each individual plant's trait values are a good indication of both its C and nutrient uptake rate and its strategy with respect to retention of those resources. The 'resource conservative' side of the LES consists of long-lived, slow-growing species that share the following traits: long leaf lifespan,

high long-term nutrient use efficiency, low leaf N and P content, low photosynthetic rates, low pH, large leaf mass per area (LMA), tough leaves of high tissue density and high dry matter content, partly due to high lignin concentrations. Species on the 'resource acquisitive' side of the LES are mostly shorter-lived and fast-growing and have the opposite values for the aforementioned traits (Wright *et al.*, 2004; Freschet *et al.*, 2010; Onoda *et al.*, 2011; Reich, 2014).

Traits of living plants have ecosystem-level consequences even after the leaf – or the whole plant – has died. Partly due to the rather low interspecific variation in nutrient resorption efficiency during senescence (Aerts, 1996), the patterns of LES trait variation among species are largely retained in the litter and thereby have important 'afterlife' consequences for interspecific patterns of leaf litter decomposability (Table 1; Cornelissen & Thompson, 1997; Cornelissen *et al.*, 1999; Santiago, 2007; Cornwell *et al.*, 2008; Fortunel *et al.*, 2009; Liu *et al.*, 2015). Together, the LES traits of resource-conservative plants tend to result in nutrient-poor, lignin-rich, recalcitrant litter. Leaf acidity, low concentrations of base cations, and high concentrations of long-chain phenols, tannins and other secondary metabolites are often associated with this resource-conservative strategy and may also contribute to slowing down decomposition rates (Cadisch & Giller, 1997; Cornelissen & Thompson, 1997; Hattenschwiler & Vitousek, 2000; Cornelissen *et al.*, 2004, 2006; Ishida *et al.*, 2008; Coq *et al.*, 2010; Hattenschwiler & Jorgensen, 2010; Makkonen *et al.*, 2012; Zanne *et al.*, 2015).

Recently, the LES has been extended to include the resource economy of all vegetative plant organs including stems and roots, summarised for the first time using data for a subarctic flora as the PES (Freschet *et al.*, 2010), and subsequently for other biomes (Fortunel *et al.*, 2012; Mommer & Weemstra, 2012; Stahl *et al.*, 2013; Pietsch *et al.*, 2014; Reich, 2014). For the fine (distal) organs such as leaves, twigs, branches and fine roots of subarctic plants, the PES and its component traits have been shown to have consistent predictive linear relationships (i.e. regression slopes) of interspecific variation in the decomposability of these organs (Freschet *et al.*, 2012a; see also Freschet *et al.*, 2013). For thick tree trunks, however, other (e.g. size-related) factors may interfere with or overrule such relationships. In tropical, temperate and global analyses, leaf vs coarse wood traits and decomposability across multiple tree species were poorly if at all correlated (Chave *et al.*, 2009; Pietsch *et al.*, 2014; Zanne *et al.*, 2015). Moreover, C and nutrient economics traits, such as lignin concentration, nutrient concentrations and wood density, tended to be relatively weak predictors of interspecific variation in coarse wood decomposition rate (Weedon *et al.*, 2009; van Geffen *et al.*, 2010; Pietsch *et al.*, 2014; Zanne *et al.*, 2015). In the following we will focus on the PES of fine organs and the fine fuels derived from them before briefly revisiting the decomposability and flammability of coarse woody debris.

1. How do the PES traits that underpin decomposability relate to flammability?

Concentrations of nutritional elements and large-chain organic compounds, as well as the stoichiometry between them, may affect

Table 1 Directions and effect sizes of key litter traits with respect to decomposition rates vs surface litter flammability do not show a consistent pattern between decomposition and fire behaviour across traits

Increase in:	Decomposition	Surface fire
Chemical traits (PES)		
Cellulose and hemicellulose concentration	– (Less inhibitory than lignin) Cadisch & Giller (1997) and Sullivan & Ball (2012)	+/– Sullivan & Ball (2012)
Lignin concentration	– Cadisch & Giller (1997), Hattenschwiler & Vitousek (2000), Cornwell <i>et al.</i> (2008), Makkonen <i>et al.</i> (2012) and Grootemaat <i>et al.</i> (2015)	– Di Blasi (1998), Drysdale (2011) and Grootemaat <i>et al.</i> (2015) + Hough (1969) and Berry & Roderick (2005)
Secondary compounds (concentrations of tannins, resins, flavonoids, terpenes)	– Flanagan & Vanclve (1983) (resins), Hattenschwiler <i>et al.</i> (2005) (polyphenols) and Cornwell <i>et al.</i> (2009)	+ Ignitability; Flanagan & Vanclve (1983) (resins), Bond & Van Wilgen (1996) and Ormeno <i>et al.</i> (2009) (terpenes) – Grootemaat <i>et al.</i> (2015, 2017b) (tannins)
Leaf nitrogen concentration	+ (Early decomposition phase) Cadisch & Giller (1997), Pérez-Harguindeguy <i>et al.</i> (2000) and Cornwell <i>et al.</i> (2008)	0/– Grootemaat <i>et al.</i> (2015)
Leaf phosphorus concentration	+ Cadisch & Giller (1997), Cornwell <i>et al.</i> (2008) and Grootemaat <i>et al.</i> (2015)	– Scarff & Westoby (2008), Scarff <i>et al.</i> (2012) and Grootemaat <i>et al.</i> (2015)
Physical traits (PES/SSS)		
Litter drying out rate (at given soil moisture and air humidity; via particle diameter and tissue density) (SSS)	–?	++ Rothermel (1972), Cornelissen <i>et al.</i> (2003), Nelsson & Hiers (2008), Zhao <i>et al.</i> (2014) and Varner <i>et al.</i> (2015)
Litter particle size (projected area) (SSS)	0?	++ Scarff & Westoby (2006), Schwilk & Caprio (2011), Engber & Varner (2012) and Cornwell <i>et al.</i> (2015)
Litter particle 3-dimensionality (e.g. curliness) (SSS)	?	++ Engber & Varner (2012) and Grootemaat <i>et al.</i> (2017b)
Surface area-to-volume ratio (SA : V) (SSS)	0/+ Makkonen <i>et al.</i> (2012)	++ Rothermel (1972), Papió & Trabaud (1990), Gill & Moore (1996) and Viegas <i>et al.</i> (2010)
Leaf mass per area (LMA) or leaf dry matter content (PES, SSS)	– Vaieretti <i>et al.</i> (2005), Santiago (2007), Cornwell <i>et al.</i> (2008), Fortunel <i>et al.</i> (2009) and Freschet <i>et al.</i> (2012a)	Ignitability, fire spread; Murray <i>et al.</i> (2013) and Grootemaat <i>et al.</i> (2015, 2017a,b) +? Sustainability (higher energy content); Grootemaat <i>et al.</i> (2017a,b)
Degree of bark detachment from wood (SSS)	–/0 Dossa <i>et al.</i> (2016)	+ Gould <i>et al.</i> (2011) (flaky bark as fuel ladder)
Traits related to architecture (SSS)		
Degree of branch ramification	+/– Cornwell <i>et al.</i> (2009) and Wilson & McComb (2005)	+ Cornelissen <i>et al.</i> (2003), Schwilk (2003) and Jaureguiberry <i>et al.</i> (2015)
Dead branch or leaf litter retention	– Cornwell <i>et al.</i> (2009)	+ Schwilk & Ackerly (2001), Schwilk (2003) and Grigulis <i>et al.</i> (2005)

+, Stimulatory effect; ++, strong stimulatory effect; –, inhibitory effect; –, strong inhibitory effect; +/-, effects can be both stimulatory and inhibitory; 0, no relevant effect. Surface fire: see main text for more details about the specific flammability variables involved (main sections II and III). The left column indicates whether the traits belong to the plant economics spectrum (PES) or size and shape spectrum (SSS).

both plant flammability and decomposability, but not necessarily in consistent ways. In general, the energetic value of the different chemicals as well as the tightness of the bonds between atoms affect fire intensity (kW m^{-1}) and fire temperatures (Rothermel, 1972; Sullivan & Ball, 2012). For decomposition, the recalcitrance and perhaps the toxicity of C-rich compounds as well as their elemental stoichiometry are important to decomposers; they need to obtain these elements in the right ratios to optimise the stoichiometry of

their own body. While nutrient contents (N, P, base cations) and C : N of litter are important drivers of litter decomposition rates, their effects on fire behaviour are less clear (Table 1). A strong effect of litter N or C : N on flammability has not been reported, although Grootemaat *et al.* (2015) reported a negative effect on flame duration via its correlation with P. Leaf P content has been shown to be a fire-retardant and is already effective at low concentrations (Scarff & Westoby, 2008; Grootemaat *et al.*, 2015). Taken

together, the effects of nutrient content on decomposability vs flammability appear largely decoupled.

The energy a unit of fuel could release through complete combustion depends on its chemical composition, which varies among species (Hough, 1969; Bond & Van Wilgen, 1996; Dimitrakopoulos & Panov, 2001). Complete combustion is, however, rare, and the degree of combustion is an even more important factor determining the total amount of heat released in a fire. The degree of combustion in turn depends on factors including chemical quality, tissue density and moisture level (Alexander, 1982), along with environmental conditions such as temperature, wind speed and slope. When the energetic value of a plant per unit mass is high, combustion may take place at higher temperatures and rates than in plants with lower energetic value. However, in practice energetic value may not be as important in determining flammability of a species in comparison with other fuel characteristics, for example total mass, structure and, again, moisture content (Bond & Van Wilgen, 1996). Thus, the direct relationship between PES-related traits and flammability via energetic value is likely to be weak.

The most abundant organic compounds in plants differ in both flammability and decomposability. Sugars, cellulose and hemicellulose combust relatively easily. Sugars, often abundant in living plant material, decompose faster than cellulose and hemicelluloses (Cadisch & Giller, 1997). Lignin is even harder to degrade, due to its complex chemical structure (Kirk & Farrell, 1987), its tight association in cell walls (Swift *et al.*, 1979) and the formation of complexes with other molecules (Hattenschwiler & Vitousek, 2000). Specific enzymes (e.g. laccase or peroxidase), only produced and excreted by specific fungi, are needed to break down lignin (ten Have & Teunissen, 2001; Lynd *et al.*, 2002). A caveat is that in dry, sunny regions, where the climatic likelihood of fire may be higher, photodegradation of lignin may accelerate decomposition directly or by promoting microbial activity (Austin & Vivanco, 2006). Lignin is not easily combusted because high temperatures are needed to break the strong atomic bonds (Cornwell *et al.*, 2009; Sullivan & Ball, 2012). However, lignin-rich tissue has a high energy content (Hough, 1969) and low water storage capacity, both of which promote the combustion of wood (Berry & Roderick, 2005). At moderate fire temperatures, however (for instance at higher substrate moisture), lignin-rich tissues may be turned into char (see Introduction), which is even more recalcitrant and decomposes very slowly (Di Blasi, 1998; Hart *et al.*, 2005a; Cornwell *et al.*, 2009).

Secondary metabolites, such as tannins, flavonoids, resins and volatile oils, are used for plant defence. They generally inhibit decomposition, because of their toxicity or protein precipitation properties, which are meant to repel pathogens and herbivores and often inhibit the activity of the microbial decomposer community too (Scheffer & Cowling, 1966; Coley, 1988; Cornelissen *et al.*, 2004; Hattenschwiler *et al.*, 2005). Among these secondary metabolites, volatiles (terpenes, terpenoids) in particular increase flammability of the material due to low ignition temperatures and high energetic value (Bond & Van Wilgen, 1996; Cornwell *et al.*, 2009; Ormeno *et al.*, 2009), but tannins have been found to reduce the rate of fire spread and fuel consumption (Grootemaat *et al.*,

2017b). In boreal forests, resins in some conifer species reduce decomposition rates and promote flammability both directly and indirectly via litter accumulation (Flanagan & Vancleve, 1983). Thus, at a given climate, any vegetation shift towards conifers is likely to lead to a concomitant shift from a more decomposition-driven C turnover to a more fire-driven one.

As already explained, tissues with much long-chain secondary (defence) chemistry (lignin, tannins) tend to have high dry matter content (dry : saturated mass ratio) and LMA and both have been linked consistently with recalcitrance to decomposition (Cornelissen *et al.*, 1999; Cornwell *et al.*, 2008; Fortunel *et al.*, 2009; Freschet *et al.*, 2012a). In dry, sunny environments, some of which may be fire-prone, low LMA may also promote decomposition via a related mechanism in sunlit environments, where the contribution of photodegradation to decomposition (see earlier in this section) grows with the surface area : volume ratio across species (Pan *et al.*, 2015). Both LMA and dry matter content are also strongly correlated with tissue density (e.g. Witkowski & Lamont, 1991; Hodgson *et al.*, 2011), as related to the SSS axis (discussed in the section below). This suggests that tissue density and LMA have affinities with both PES and SSS.

III. Fire–decomposition interactions via traits in the size and shape spectrum (SSS)

There is a key role for SSS-associated traits that determine the oxygen availability in the fuel-bed and thereby especially its ignitability and fire spread rate (Table 1). This contrasts sharply with the PES traits that drive decomposition (see previous section), which are mostly related to chemical composition. There is now rather convincing evidence that the particle size and shape of fine litter, particularly of leaves, are an important factor for fire behaviour in surface fuel-beds (Rothermel, 1972; Viegas *et al.*, 2010). Small leaves tend to form dense, poorly ventilated fuel-beds that ignite with difficulty and strongly constrain fire spread, with low fire sustainability (Scarff & Westoby, 2006; Schwillk & Caprio, 2011; see also Ganteaume *et al.*, 2014 for negative effects of direct experimental fuel-bed compaction on flammability). For instance, within the gymnosperm (broadly conifer) lineage most species build highly flammable litter beds, helped by airy structure, high energetic value and ignitable secondary chemistry. However, non-*Pinus* genera within the family Pinaceae produce nonflammable litter beds because of dense stacking of their small, simply linearly shaped, individually shed needles (Cornwell *et al.*, 2015). Similar relationships as between leaf size and fuel-bed flammability might hold for fine branches, which tend to be correlated allometrically with leaf size across woody species (Westoby & Wright, 2003). If so, and in the absence of strong nonadditive interactions between species and between organs (but see section V), the range of combinations from small leaves and twigs to large leaves and twigs will amplify the impact of species composition on forest floor ventilation and flammability.

Some initial studies have now also explicitly shown the important role of leaf morphological traits, especially leaf ‘curliness’, as a promoter of fuel-bed ventilation and flammability (Engber & Varner, 2012; Grootemaat *et al.*, 2017b) while shoot

branching pattern and degree of ramification are likely to play a similar role (Cornelissen *et al.*, 2003). Thus, it is probably the combination of litter particle size and shape that, via relative 'three-dimensionality' (Table 1), promotes flammability principally through fuel-bed ventilation.

Moreover, these morphological traits may also promote ignitability, fire spread rate and sustainability indirectly through faster drying-out rates of the litter layer at given environmental moisture (Table 1; Cornelissen *et al.*, 2003), as litter obviously burns better the drier it gets (Plucinski & Anderson, 2008; Ganteaume *et al.*, 2009; Blauw *et al.*, 2015; Varner *et al.*, 2015; Simpson *et al.*, 2016). Depending on the time since the last rain event, species may vary greatly in their actual moisture content dependent on litter layer structure but also internal tissue density (Nelsson & Hiers, 2008). For instance, Zhao *et al.* (2014) found that time to 50% water loss of saturated temperate tree twig litter varied between 3 and 55 h dependent on wood density, which in turn depended (inversely) on decomposition stage and tree species. Generally, denser twigs had poorer ignitability and burned longer, but these relationships depended on the moisture content.

Related to the size and relative three-dimensionality of litter particles is their surface area to volume ratio (SA : V), a trait that has been considered to be a key contributor to fuel-bed ignitability and subsequent fire spread rate (Rothermel, 1972; Papió & Trabaud, 1990; Ganteaume *et al.*, 2009; Viegas *et al.*, 2010; van Altena *et al.*, 2012; Simpson *et al.*, 2016). Also, higher LMA implies a lower area to volume ratio (see above) giving it lower ignitability, as Murray *et al.* (2013) and Grootemaat *et al.* (2015, 2017b) showed across a vast array of southeast Australian plant species. Thicker leaves with low SA : V ratio require more heat to ignite and combust, because they take longer to dehydrate and, within fuel-beds, can be starved of oxygen related to dense packing (see above; Bond & Van Wilgen, 1996). At higher tissue density and upon oxygen-limitation, combustibility will be compromised, especially in woody debris, as the material may smoulder rather than flame, with a high likelihood of charring. Higher density woody litter also dries out more slowly (Zhao *et al.*, 2014), which should inhibit ignition and fire spread. However, at a given SA : V the fuel-bed may vary in bulk density dependent on LMA (or mass per area of nonleaf litter), which in turn is determined by litter particle thickness and/or tissue density; these factors may bear on fire combustibility and sustainability (Grootemaat *et al.*, 2017b).

Contrasting with the key roles of litter particle size and SA : V in fuel-bed flammability, no clear connection between litter particle size and decomposability across land plant species has, to our knowledge, been shown. Makkonen *et al.* (2012) did find a slight positive effect of litter-bed SA : V ('3D structure') on decomposability in combination with other traits across diverse species from wide-ranging biomes. In general, however, it seems that better accessibility of the litter tissues to decomposers as determined by the higher area to volume ratio of smaller particles is a much less important factor for decomposability than the chemical and structural quality of the tissues themselves (but see below for coarse woody debris).

As already mentioned, leaf or litter moisture content is an important inhibitor of ignitability, fire sustainability and combustibility partly by keeping the fire temperature low as evaporation costs energy (Bond & Van Wilgen, 1996; Dimitrakopoulos & Papaioannou, 2001; Zhao *et al.*, 2014). By contrast, high litter moisture enhances decomposition by improving the microclimate for the microbial community (Richter *et al.*, 2000; Wardle *et al.*, 2003; Hart *et al.*, 2005b; Makkonen *et al.*, 2012). Particularly interesting is how litters of different species and organs vary in moisture content (related to their internal tissue structure and consequent drying-out rate) at given (low) environmental moisture, that is, as a species-specific trait. While living plant parts vary greatly and consistently in moisture content across species even at a given moisture availability (e.g. Simpson *et al.*, 2016), litter moisture varies less at given environmental moisture, as dead plant material can logically no longer regulate its water content. Yet, variation in litter moisture among litter species at given air-dry conditions may be relevant to fire behaviour in the field. For instance, among 72 leaf litter species from northern Sweden, equilibrium moisture content at standard lab conditions (*c.* 50% relative humidity, 20°C) was on average 5.3%, but ranged widely from 1.5% in *Carex saxatilis* to 19% in *Picea obovata* (J. H. C. Cornelissen, unpublished). There is some evidence that such a moisture ranking, all else being equal, would have the opposite effect on decomposition rates, that is, higher tissue moisture content inhibiting fire but promoting decomposition fire. For instance, leaf litter from seven temperate tree species in Japan varied in moisture content both within and between litter layers of different moisture levels, with the moister litter species generally providing a more favourable substrate for decomposers and thus showing higher microbial respiration rates (Ataka *et al.*, 2014).

Branching architecture may affect both decomposition and fire behaviour in other ways than via the effect of fuel-bed ventilation. When a tree falls, the three-dimensional branching pattern may prevent most of the canopy from touching the ground, thereby inhibiting its own decomposition through lack of exposure to the soil decomposer community and lower moisture (Wilson & McComb, 2005; Cornwell *et al.*, 2009). On the other hand, such a configuration may also keep the air and soil beneath the fallen tree more humid (Scholes & Archer, 1997), promoting decomposition of the litter layer below it and slowing fire spread. However, under very dry conditions vertical 'connectors' of tree canopy and surface litter may provide fire ladders that enable fire to spread more quickly to surrounding vegetation. If (living or dead) branches or (flaking) bark of standing trees extend downward close to the forest floor, a fire can climb towards the tree crown, the so-called 'torching' or 'crowning' effect, changing the fire type from surface fire to crown fire (Schwilck, 2003; Pausas *et al.*, 2004; Hoffmann *et al.*, 2012). For example, *Picea mariana* has a high probability of developing a crown fire, due to the branches' ladder structure (Shetler *et al.*, 2008). It thus affects the fire regime in boreal forests where it dominates.

Retention of dry dead wood and leaves still attached to dryland trees, shrubs or savannah grasses (Grigulis *et al.*, 2005; Cornwell *et al.*, 2009) also promotes wildfire, partly directly and partly by enabling fire to reach canopies. This dry material ignites quickly

and the heat released can dry out the surrounding live plant material, facilitating fire spread (Bond & Van Wilgen, 1996; Schwilk, 2003). However, this dead material is out of reach for the soil microbial community and cannot be decomposed easily. Thus, increasing biomass proportions of vegetation that are retained as standing dead branches and fine litter might change a community from more decomposition-driven to more fire-driven.

1. Decomposition–fire interactions via PES and SSS traits for different plant organs

In general, coarse woody debris (CWD; diameter > 5 cm) decomposes more slowly than fine stems (twigs; usually < 2 cm in diameter), which in turn decompose more slowly than leaves (Dearden *et al.*, 2006; Freschet *et al.*, 2012a, 2013; Zanne *et al.*, 2015). This can partly be explained by PES-related traits. Wood contains much more lignin, making woody litter less decomposable than leaf litter (Swift *et al.*, 1979; Freschet *et al.*, 2012a; Magnusson *et al.*, 2016). Furthermore, wood has a much higher C : N, at 200–1200 : 1 (Cornwell *et al.*, 2009; Weedon *et al.*, 2009), than leaves, at 25–75 : 1 (Swift *et al.*, 1979), making the leaves more decomposable. However, even for a given lignin content or PES trait combination, coarse wood decomposes more slowly than twigs, and twigs more slowly than leaves (Freschet *et al.*, 2012a). Thus, the lower decomposability of woody litter may be understood partly from traits in the SSS. In particular, coarser material has lower surface area to volume ratio, providing poorer access to decomposers. In a tropical study, logs of tree species with larger trunk diameters tended to be decomposed more slowly in broadly the same forest environment (van Geffen *et al.*, 2010). When trees fall down they may shatter, depending on mechanical properties such as fibre configuration. This fragmentation enhances both the amount of substrate in contact with the soil and the total surface area to volume ratio, which can enhance both decomposition and fire spread (Wilson & McComb, 2005; Cornwell *et al.*, 2009).

Also, leaves and fine stems, with their lower LMA and higher SA : V, tend to ignite more swiftly, while CWD, with its high lignin content and energetic value, typically ignites less easily but burns or smoulders longer once ignited (Volokitina & Sofronov, 2002). Tissue density is higher in CWD than in leaves. Wood density may only be indirectly related to decomposition rates (Weedon *et al.*, 2009) and fire (Cornwell *et al.*, 2009; Zhao *et al.*, 2014), that is, via its relationship to diameter, wood chemistry, anatomy and moisture (see above).

Bark is a woody plant part of particular interest in the context of both decomposition and fire. While constituting only a small mass proportion of CWD in most ecosystems, bark may have disproportionately large effects on these C release processes. In addition, bark shed from eucalypt species in Australia is known to contribute massively to the litter layer (*c.* 20–45%; McColl, 1966; Woods & Raison, 1983; Lamb, 1985). Among PES-related traits, the secondary chemistry, with its often high lignin, resin, suberin and/or phenolic content, makes bark recalcitrant to decomposition; on average the decomposability of bark litter is even somewhat lower than that of coarse wood (*i.e.* xylem) across wide-ranging temperate tree species (R. Roos & J. H. C. Cornelissen,

unpublished), and much lower than that of leaf litter for 10 Australian woody Myrtaceae species (Grootemaat *et al.*, 2017a). There was also great variation in bark decomposability among species in the latter study, which was mainly predicted by PES-related traits, principally initial lignin concentration, as known from leaf litter (see above). By contrast, bark litter flammabilities were predicted by different PES- and SSS-related traits among the same species, depending on experimental procedures and flammability parameters studied. In experimental burnings of individual bark pieces ignitability was higher in species with higher [N] while flame and smoulder duration (fire sustainability) were positively related to bark particle size (*i.e.* mass) and flame duration negatively by [P] (Grootemaat *et al.*, 2017a). By contrast, in experimental burnings in bark litter fuel-beds of seven *Eucalyptus* species plus the close relative *Angophora costata*, six of which overlapped with the above study, the size and thickness of bark particles were good predictors of fire spread rate and duration. Small and thick particles gave dense packing (*i.e.* poor ventilation) and high bulk density, leading to slow fire spread and low fire temperatures but long (smouldering) fire duration (J. Molleman *et al.*, unpublished). In the above-mentioned Australian tree species bark is shed profusely, leaving substantial bark litter layers on the forest floor. Also, bark ribbons hanging down from trees have been associated with the fuel ladder effect, helping surface fires to climb into the canopy (Gould *et al.*, 2011). The role of litter bark thickness for flammability is interesting for another reason. While still attached to trunks and branches, thick bark is well known to protect the inside structures of living trunks against heat (Cornelissen *et al.*, 2003; Bauer *et al.*, 2010; Pausas, 2015) besides additional functions such as structural support and transport of photosynthates (Rosell, 2016). In coarse woody debris, attached barks can create a favourable, moist microclimate in the wood enclosed (Cornwell *et al.*, 2009; Dossa *et al.*, 2016), resulting in 2.4-fold faster decomposition compared to logs of the same species with bark removed (Ulyshen *et al.*, 2016). Yet, in some species the disappearance of bark may promote wood decomposition, partly via attack by (long-horn) beetles (our observations) or have no effect (Dossa *et al.*, 2016).

IV. Integrating decomposition–fire interactions: decoupling of PES and SSS effects?

From the evidence presented so far, summarised in Table 1, it is clear that species rankings of litter decomposability and several flammability parameters are mostly uncoupled. Indeed, all combinations of positive, negative and neutral trends are seen for trait–decomposability vs trait–flammability relationships, depending on the traits involved. In general the traits involved in the PES tend to be important drivers of interspecific variation in litter decomposition rates, especially for leaves. By contrast, while (only) for leaves in isolation PES-related traits are important drivers of their flammability, SSS traits tend to be the most important drivers of interspecific variation in litter-bed flammability, especially in fire spread rate and sustainability. For CWD and twigs both PES traits (*e.g.* lignin and nutrient content) and SSS traits (*e.g.* diameter) appear to be important drivers of decomposition rates, while both PES traits and SSS traits are also important for flammability but in

apparently disconnected ways (e.g. lignin for fire sustainability; log, branch or twig dimensions and branching architecture for fire spread; wood density for fire spread and sustainability partly via water relations).

This review is an invitation to check empirically how the various trait–process relationships described above play out in terms of interspecific ranking of decomposability vs flammability in specific contexts. As a first example (Fig. 3) a direct comparison of 15 temperate plant species, varying widely in phylogenetic position and growth form, supports our hypothesis, that is, that leaf decomposability (as tested in a ‘common garden’ litter-bed experiment) and several litter-bed flammability parameters are largely decoupled. Indeed, there was no consistent decomposability–flammability relationship between growth forms or between species within growth forms. Correspondingly, Grootemaat *et al.* (2015) found that leaf decomposability among wide-ranging perennial Australian species was largely decoupled from flammability at the single leaf level. This was mirrored by the study on bark litter mentioned above, where bark decomposability and flammability were largely unrelated across 10 Australian species (Grootemaat *et al.*, 2017a). There seems, however, to be some coupling of decomposability and flammability at the crude level of leaves vs twigs vs CWD (as opposed to across different plant species), with leaf litter being generally more decomposable, more ignitable and promoting fire spread but having lower fire sustainability than CWD and with twigs taking an intermediate position. Because of the different chemical and physical properties of coarse wood, bark, twigs and leaves, the biomass allocation pattern of these organs in different species may thus affect both decomposition (Freschet *et al.*, 2013) and fire in specific ways.

V. From species to communities: are litter interactions for decomposition and fire behaviour connected?

Flammability and decomposability of a system cannot always be deduced simply from the sum of the traits of the different species, partly because of possible nonadditive interactive effects within the plant community (Suding *et al.*, 2008). Litter of different plant species has shown nonadditive mixture effects on C release processes, but with a strong difference between the magnitudes of mixing effects on decomposition vs those on flammability. Mixtures have been shown to have positive, neutral or negative effects on decomposition rates as compared to expected values based on monospecific litters (Hoorens *et al.*, 2003; Hattenschwiler *et al.*, 2005; Nilsson & Wardle, 2005; Jonsson & Wardle, 2008; Keith *et al.*, 2008; Pérez-Harguindeguy *et al.*, 2008; Coq *et al.*, 2010; Freschet *et al.*, 2012b; Cuchietti *et al.*, 2014). Remarkably, these and other studies have tested many intuitively likely explanatory environmental factors for their potential effect on nonadditivity, but none of them has been found to have substantial and consistent predictive power. These nonadditive effects, while often statistically significant, tend to be idiosyncratic based on the particular species combinations. Furthermore, their effect sizes, in a given environment, are broadly an order of magnitude smaller than interspecific variation in decomposition

rates. Arguably also, a key effect of litter mixing besides changes in mean decomposition rate may be reduction in the variability of process rates and thus the stability of the decomposer system (Keith *et al.*, 2008).

The generally limited effect of litter mixing on decomposition rates contrasts strongly with nonadditivity for fire behaviour in litter mixtures. While fire spread rate and mass loss rate in mixed fine fuels can to some extent be predicted from the mass fractions and physical properties of individual fuel types (Viegas *et al.*, 2010),

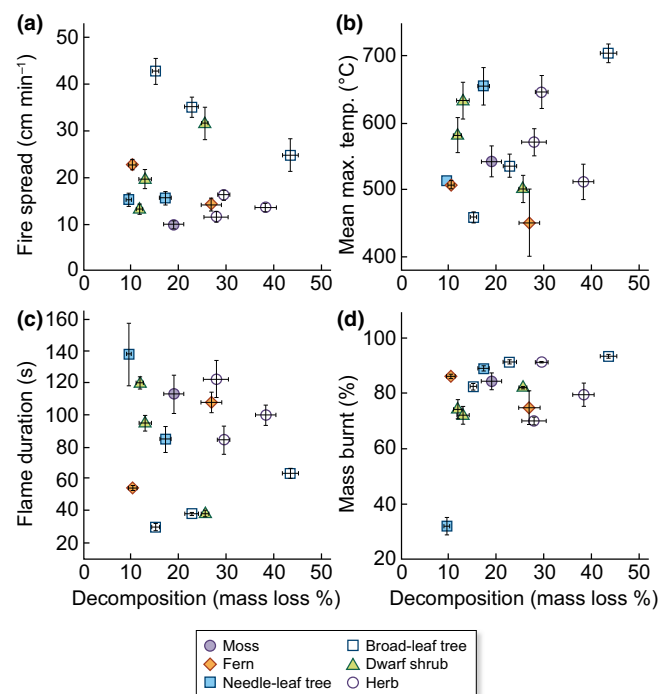


Fig. 3 Preliminary experimental test of the hypothesis that leaf litter decomposability (x-axis) and flammability (y-axis) should be largely decoupled across species, as conceptualised in Fig. 2. The results are from a study (J. H. C. Cornelissen & J. Veenboer, unpublished) in which 14 Dutch temperate species, of wide-ranging phylogenetic position and growth form, were tested for leaf-litter decomposability and four flammability parameters: (a) fire spread rate, (b) mean maximum fire temperature, (c) duration of flaming phase and (d) percentage of initial mass burnt. Leaf litter was collected freshly senesced from (semi-)natural sites in the Netherlands in November 2009. Decomposability is expressed as mean percentage mass loss of leaf litter (\pm SE) during 15 wk of simultaneous incubation in 1 mm mesh litterbags ($n = 10$ per species) in an outdoor litterbed at VU University Amsterdam from 12 February 2010. The methodology broadly followed Cornelissen (1996). The litterbags were incubated 5 cm deep inside a 10 cm deep mixed leaf litter matrix in the litterbed (6 cm after gradual compaction), which had been collected from the surface of several woodland and herbaceous habitats, thoroughly mixed and spread out on a well-draining, bare sand base. The experimental burns, in a fire basket in the Fire Laboratory Amsterdam for Research in Ecology (FLARE), followed the methodology described by van Altena *et al.* (2012). The litter fuelbeds were 25 cm in diameter and 3 cm deep. For the two ericaceous dwarf shrubs we used terminal foliated stems in the fuelbed instead of individual leaves. Species means (\pm SE) are given. The species include: one moss (*Polytrichum commune* Hedw.); two ferns (*Dryopteris carthusiana* Vill., *Pteridium aquilinum* L.); two needle-leaf trees (*Larix decidua* Mill., *Pinus sylvestris* L.); four broadleaved trees (*Alnus glutinosa* L., *Fagus sylvatica* L., *Ilex aquifolium* L., *Quercus robur* L.); two ericaceous dwarf shrubs (*Calluna vulgaris* L., *Erica tetralix* L.); and three herbs (*Chamerion angustifolium* L., *Artemisia vulgaris* L. and the semi-herbaceous scrambler *Rubus fruticosus* L.).

recent experimental studies have demonstrated very strong positive and more modest negative interactive effects of species mixing in litter fuel-beds (as compared to expected values based on monospecific fuel-beds) for ignitability, fire spread rate and fire intensity (de Magalhaes & Schwilk, 2012; van Altena *et al.*, 2012; Zhao *et al.*, 2016). Usually the enhancing effects were explained by dominance of the more flammable species in the mixture for a given fire variable. Suppressing effects could be due to, for instance, small and simple leaves filling up the spaces between the partner litter particles, thereby strongly inhibiting oxygen availability and ignition success or fire spread rate and sustainability (Zhao *et al.*, 2016). Recently, Blauw *et al.* (2015) added litter moisture content as an important explanatory factor for nonadditivity in flammability of temperate litter mixtures. Both the mean and the variance in nonadditivity increased strongly with increasing litter moisture content (and from mostly positive to mostly negative effects). Variance increased because at high (30%) moisture the threshold for successful ignition and fire spread was approached. This variance is ecologically relevant, as even a single successful ignition out of many can have great ecological impact in the field. It also contrasts with the variance stabilising effect of litter mixing on decomposition rates mentioned above. In the above two studies some species were much more often involved in nonadditivity than others, suggesting that, unlike for decomposition, certain plant traits may have more general predictive power of nonadditivity. However, more empirical data are needed in this new field before general conclusions may be drawn. What we can already imply is that, because of the idiosyncrasy and rather small effect sizes of nonadditivity in decomposition rate vs the large effect sizes in flammability (probably underpinned by PES traits), the direction and magnitude of mixture effects for decomposition vs fire behaviour are probably decoupled across coexisting species in nature.

To add further complexity, many plant communities not only host vascular plants but also phylogenetically distant nonvascular autotrophs, especially bryophytes and lichens, both known to differ greatly in secondary chemistry from vascular plants. These differences have important consequences for their contributions to decomposition and fire behaviour. In boreal and subarctic regions bryophytes and lichens form a large part of the vegetation biomass. Bryophyte litter decomposes slowly, partly because of unfavourable environmental conditions but also because of its recalcitrant chemical content (Cornelissen *et al.*, 2007a; Lang *et al.*, 2009; Woodin *et al.*, 2009). As a consequence, organic material accumulates, forming deep organic layers, increasing fire fuel loads. Moreover, lichens often contain highly ignitable chemicals. The predominance of C-rich secondary compounds of high energetic value in bryophytes and lichens, together with their fast desiccation rates related to their ectohydric physiology, promotes flammability of the boreal and subarctic system as a whole. The fact that *Sphagnum* peat in boreal forest burns poorly is due to generally wet conditions rather than its fuel quality (Shetler *et al.*, 2008). Fire regimes appear to be changing under conditions of a warming climate, with occasional prolonged dry periods and increasing fire frequency and intensity. Given the thick layers of organic fuel, this may lead to strongly increasing C emissions with significant

consequences for the regional and perhaps even global C balance (van der Werf *et al.*, 2010; Mack *et al.*, 2011; IPCC, 2012, 2013). A large unknown in this context that merits in-depth study is the influence of the – often strong – interactions (i.e. nonadditivity) between bryophytes and vascular plants on both decomposition (Wardle *et al.*, 2003) and fire behaviour (Blauw *et al.*, 2015).

VI. Feedbacks between community (trait) composition, decomposition and fire

Because fire and decomposition tend to be influenced by different plant traits, or in different ways by the same traits among species sets, these two processes will be affected by plant community composition in different ways. Assembly theory (Keddy, 1992) may help to better understand whether and how (much) decomposition and fire are coupled via traits at the community scale. One aspect of assembly theory, habitat filtering, describes how the local environment constrains the range of trait values and thus species. Both the rate of decomposition and the fire regime affect this assembly process, and because they are in part the result of the traits of the living species, this forms a feedback loop (Chapin *et al.*, 2011), which can now be considered in light of research progress on the major axes of plant functional variation discussed above. With respect to litter decomposability, a lot is known of the drivers of the traits associated with the PES that underpin decomposability: low LMA, low lignin and high leaf N contents are associated with high soil fertility (Ordonez *et al.*, 2009; Fujita *et al.*, 2013; Maire *et al.*, 2015) and soil moisture content – waterlogged conditions excluded (Verheijen *et al.*, 2013). These trait values are associated more with temperate than tropical conditions (Makkonen *et al.*, 2012; van Bodegom *et al.*, 2014).

The connections between community assembly and the SSS-associated traits in different environmental settings have been explored to a lesser extent. Some of the better understood patterns seem to relate understandably to temperature and moisture regimes. For instance, leaves are generally smaller in cold, dry or nutrient-poor environments (Parkhurst & Loucks, 1972; Orians & Solbrig, 1977; Körner *et al.*, 1989). Bark thickness, a determinant of flammability (see above) has been shown to increase with prevalence of drought and high annual temperatures (Laughlin *et al.*, 2012) and is generally recognised as an important trait determining fire resistance (Higgins *et al.*, 2012; Hoffmann *et al.*, 2012). It is also used – currently as one of the few traits – to determine fire resistance of plant functional types in global models (Hantson *et al.*, 2016). Likewise, leaf and litter moisture contents decrease with increasing drought and are also used in global fire modelling (Hantson *et al.*, 2016). Branching pattern, important for fuel-bed ventilation and flammability (see above), is known to be linked to light environment. Dense crowns with strong ramification into short lateral axes bearing smaller leaves tend to be predominant in sunny environments, while open crowns with sparse long branches bearing larger leaves are associated with shade (Cornelissen, 1993).

While some have argued that variation in fire response traits and in traits that underpin flammability are generally not linked across species (Lavorel & Garnier, 2002), others did find such correlations

(Grigulis *et al.*, 2005; Pausas & Keeley, 2009; Romero *et al.*, 2009). For instance, among pines (*Pinus* spp.), dead branch retention is evolutionarily correlated with fire-dependent seedling recruitment (Schwilk & Ackerly, 2001; Schwilk, 2003), suggesting a positive feedback between fire-promoting and fire-survival traits. Also, in semi-arid Australian woodlands, re-sprouters had larger leaves and a more open and flammable litter layer compared to obligate post-fire seeders (Scarff & Westoby, 2006).

Community assembly, together with direct biotic interactions (including litter interactions, see above) adds real-world complexity to the balance between decomposition and fire prevalence. This balance is further influenced by several crucial feedbacks, with fire and decomposition also playing a large role in shaping the plant community (Bond & Keeley, 2005; Bond *et al.*, 2005; Hart *et al.*, 2005b; Hattenschwiler *et al.*, 2005; de Deyn *et al.*, 2008; Pausas & Verdu, 2008). Surface fire and decomposition are not only connected through species (trait) composition but also via litter quantity (Smithwick *et al.*, 2005; Ziska *et al.*, 2005; Balch *et al.*, 2008) and the spatial distribution of the species within the plant community (Bond & Midgley, 1995; Schwilk, 2003; Pausas *et al.*, 2004). Litter quantity is also driven by productivity which in turn depends on community composition and abiotic drivers (Fig. 1a,b). Although traits of a single plant individual are unlikely to influence flammability or decomposability of an ecosystem, the traits of the dominant species in an ecosystem are important drivers of C cycling (Grime, 1998; Chapin, 2003; Suding *et al.*, 2008), partly because they determine ecosystem-level decomposability and flammability. An interesting example of positive feedback between fire and decomposition is that of the invasive resprouting grass *Ampelodesmos mauritanica* in Spain (Grigulis *et al.*, 2005); as well as via other invasive grasses in Hawaii, parts of Australia and southwest USA (our observations). *A. mauritanica* replaces native shrublands because of its resprouting strategy, faster growth and larger biomass. Fuel loads increase even more through litter accumulation, because *A. mauritanica*

decomposes 30% slower than native species. It is also more flammable than native shrubs due to high leaf dry matter content and fine texture (promoting oxygen supply and quick drying of litter) and a continuous fuel-bed. These traits together stimulate fire frequency and promote the abundance of this grass, but slow down decomposition rates (Fig. 2, top left corner). Correspondingly, dry grass-dominated tropical savannah generally tends to have persistently higher fire frequency, intensity and/or severity than tree-dominated savannah or forest in the same region (Hoffmann *et al.*, 2012).

Fire can change the community and related traits directly or indirectly by changing soil conditions (Fig. 1a). For instance, the ashes remaining after wildfire often greatly increase soil fertility (Marion *et al.*, 1991), thereby promoting fast-growing, nutrient-demanding species during post-fire succession (Wardle, 2002). The traits associated with a nutrient-acquisitive strategy also promote the decomposability of the litter derived from leaves, twigs and fine roots of such plants, as discussed above, leading to positive vegetation feedback to fertility during early succession. Moreover, ashes often have lower N : P ratio compared to pre-fire vegetation (and its litter) (Niemeyer *et al.*, 2005) owing to release of N into the atmosphere even at lower fire temperatures (Evans & Allen, 1971). The temperature dependence of N losses relative to P losses implies that litter traits that promote lower fire temperature (especially higher moisture content; see above) may also reduce the post-fire soil N : P ratio. And, as for fertility in general, soil N : P ratio may impact litter decomposition via differential traits of plant species and microbes adapted to N vs P limitation of growth and decomposition processes (Koerselman & Meuleman, 1996).

Decomposition affects community composition and plant traits mainly via nutrient availability but also by modifying moisture levels, such as through reduction of tissue density (see above; Fig. 1b). Plant communities have certain properties that are the outcome of the combination of species traits. Examples are vegetation albedo, respiration, canopy roughness and

Table 2 Ecosystems contrast greatly in their combination of flammability and decomposability

Ecosystem	Flammability	Decomposability	Characteristics
(Semi-)Desert	Low	High	Sparse plants with sometimes succulent leaves, small and discontinuous fuel-bed (Bond & Van Wilgen, 1996)
Savannah/seasonal forest	High	High	Grasses with high surface area to volume ratio, continuous fuel-bed, high productivity (Bond & Van Wilgen, 1996; Bond <i>et al.</i> , 2005; Grigulis <i>et al.</i> , 2005)
(Mediterranean) Shrublands	High	Low	Dense shrubs with fine leaves, mostly growing under dry abiotic conditions; continuous (elevated) fuel-bed; usually crown fire systems (see Bond <i>et al.</i> , 2005)
Broadleaved forest	Low to high	High	Trees with different heights and understorey (depending on soil and climate); in dry sclerophyll forest (Australia) bark forms an important component of the litter layer. Mix of crown fire and surface fire systems
Boreal forest	High	Low	Trees with fine branches and leaves, often with high terpene levels; thick continuous fuel-beds (Bond <i>et al.</i> , 2005; de Deyn <i>et al.</i> , 2008). Mix of crown fire and surface fire systems
Tundra	Medium	Low	Flammable species (mosses, lichens) but unfavourable abiotic conditions for fire and low fuel load (Swift <i>et al.</i> , 1979)

Note that these ecosystems are illustrative end points of gradients in physiognomy, and as such many of the plant trait effects may be most important along the gradients. For example, the discontinuous surface fuels in semi-desert often will not carry surface fires and the surface fuels in savannah almost always will, but in between these extremes, there are marginal fuel beds where fire may only sometimes spread. For these marginal fuel beds, plant traits may have the most profound effect on the spread (or lack of spread) of a surface fire.

evapotranspiration of the plant community (Shaver *et al.*, 2000; Chapin, 2003). These properties play an important role in determining temperature and moisture conditions of the local environment, which in turn influence fire behaviour and decomposition rates. After fire, plant communities will have changed albedo and evapotranspiration, depending on pre-fire conditions, fire severity and time after fire. For example, a regional-scale shift from forests to grasslands after fire increases albedo and decreases evapotranspiration, which is accompanied by higher surface temperatures and lower precipitation (Snyder *et al.*, 2004; Montes-Helu *et al.*, 2009). There may be further feedbacks via changes in rooting depth with species shifts; species that can tap into the water table will maintain a higher water content in their tissues, thereby reducing their flammability. Moreover, the relative importance and effects of decomposition and fire may change over time in a community. For example, depending on the stage of succession of a community after fire, fuel loads and decomposability of the system will differ. Boreal forests in Canada with different fire-free intervals had different plant community composition, dead wood loads and organic layer depths (Johnstone, 2006), which in turn affected fire behaviour and decomposition.

VII. Conclusion

Plant trait spectra make important contributions to decomposition and fire regimes, setting up a two-dimensional space that describes both the pathways and the flux rates for C flow from biosphere to atmosphere (Fig. 1). As discussed above, these contributions must be shaped strongly by the environmental context. Yet, this review has demonstrated that the traits of living plant organs, especially those forming part of the PES vs SSS, are strongly linked to litter dynamics and, thereby, ecosystem C budgets. As such, the assembly mechanisms which determine the traits of the community also affect litter dynamics, both decomposition rate and flammability. Because of the general tendency for variation in PES and SSS traits to be at least partially uncoupled across species, in answer to our central question, there is ample scope for all four combinations of decomposition and fire regimes in Fig. 2 to occur in the real world (see Table 2). This review is an invitation to researchers worldwide to collect data for litter traits, and their weighted abundance, for different ecosystems in the real world to test and quantify how these regimes can be understood and predicted (see also Dias *et al.*, 2017). While there is already a substantial but largely incomplete body of data available in the literature for PES traits, databases are almost empty as far as SSS-related litter traits for different plant organs are concerned – even though litter particle size may partly be derived from green leaf size, which has higher availability (Kattge *et al.*, 2011).

There may also be more subtle PES and SSS effects on surface litter dynamics, via small changes in plant community composition or their interactions with abiotic regimes as well as via species mixture effects, especially for fire. While great challenges lie ahead especially for predicting future fire regimes worldwide (Macias-Fauria *et al.*, 2011; Harris *et al.*, 2016), our new concept will contribute to a better understanding of the impacts of environmental changes, such as those driven by climate or land-

use change as well as by invasions of new species into existing communities, on decomposition and fire regimes and ecosystem C dynamics.

Acknowledgements

This review benefited from grant 047.018.003 by the Netherlands Organisation for Scientific Research (NWO), from discussion with Henk Schat and Ian Wright, and from advice and assistance of the FLARE team at Vrije Universiteit and especially Richard van Logtestijn and MSc students Jochem Veenboer and Jasper Molleman.

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