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RESEARCH ARTICLE

Experimental evidence that leaf litter decomposability and flammability are decoupled across gymnosperm species

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Abstract

1. Biological decomposition and wildfire are two predominant and alternative processes that can mineralize organic C in forest litter. Currently, the relationships between decomposition and fire are still poorly understood.
2. We provide an empirical test of the hypothesized decoupling of surface litter bed decomposability and flammability, and the underlying traits and trait spectra.
3. We employed a 41-species set of gymnosperms of very broad evolutionary and geographic spread, because of the wide range of (absent to frequent) fire regimes they are associated with.
4. We found that the interspecific pattern of mass loss proportions in a “common garden” decomposition experiment was not correlated with any of the flammability parameters and an RDA analysis also showed that the decomposability and flammability of leaf litter in litter layers were decoupled across species. This decoupling originates from the former depending mostly on size and shape spectrum traits and the latter on PES traits and those trait spectra being virtually uncorrelated.
5. *Synthesis*: Our results show that, indeed, leaf litter decomposability and flammability parameters are decoupled across species, and this decoupling can be explained by their different drivers in terms of trait spectra: chemical traits for decomposability and size-shape traits for litter layer flammability.

KEYWORDS
biogeochemical cycling, decomposition, fire ecology, flammability, leaf litter quality, leaf shape, plant functional traits

1 | INTRODUCTION

Forests provide multiple ecosystem services (van der Plas et al., 2018), including climate regulation by storing C from the atmosphere in living and dead plant matter (Canadell & Raupach, 2008; Pan et al., 2011). In turn, the turnover of this plant matter, involving different pathways of C release from plant litter, are important for this forest function (Cornwell et al., 2008). In the soil surface litter layer, biological decomposition and wildfire are the two predominant and alternative processes that can mineralize organic C in forest litter, and return it to the atmosphere. Biological decomposition returns litter C to the atmosphere at a relatively slow rate. On the other hand, leaf litter is an important fuel for forest surface fires, and through combustion, fire returns litter C to the atmosphere in a very fast but episodic way (Bowman et al., 2009; Cornwell et al., 2009; Grootemaat et al., 2015; Hyde et al., 2011). Decomposition reduces the amount of fuel available for combustion, and it also reduces the internal density of single leaf litter or coarse woody debris, thereby promoting fuel internal ventilation and flammability. At the litter bed scale, as decomposition progresses, fragmented litter particles with smaller sizes may build denser litter beds. This in turn limits fuel-bed ventilation and flammability (Scarff & Westoby, 2006; Zhao et al., 2014, 2018). Likewise, fire reduces the amount and alters the quality of substrate available for decomposition. Thus, both processes affect each other indirectly.

However, as decomposition and fire differ in the frequency and speed of carbon release, and are each studied by their specific research methodologies and communities, the relationships between decomposition and fire are still poorly understood (but see Grootemaat et al., 2015; Zhao et al., 2014, 2018). In particular, to improve predictions of carbon release from different ecosystems, it is important to know whether and how litter decomposability is linked with its flammability across species, and which traits and trait spectra underlie this relationship. In a Tansley Review, Cornelissen et al. (2017) asked and dissected this question through a conceptual model, based on two distinct trait spectra: the 'plant economics spectrum' (PES) and the 'size and shape spectrum' (SSS). The biochemistry traits driving litter decomposability of different fine organs across species were linked to the PES, which has its origin in the 'leaf economics spectrum' (Diaz et al., 2016; Wright et al., 2004) and was then extended into the spectrum for fine organs (e.g. leaves, stems and roots; see Freschet et al., 2010; Reich, 2014). In the meantime, PES traits can also influence (enhance or inhibit) plant flammability to some extent (Archibald et al., 2019; Ormeño et al., 2009; Popović et al., 2021; Scarff & Westoby, 2008; Varner et al., 2015). The SSS, comprising litter particle size and shape and their consequent effect on fuel bed structure and aeration, was linked with interspecific variation in flammability parameters. In their conceptual review, Cornelissen et al. (2017) demonstrated that PES-related biochemical traits (concentrations of nutritional elements, large-chain organic compounds and the stoichiometry between them) may affect both litter flammability and decomposability, but not necessarily in consistent ways. In contrast, the species effect on litter flammability should be strongly controlled by oxygen availability through SSS-related morphological traits. Based on that, they hypothesized that interspecific variation in litter decomposability should be decoupled from that in litter-bed flammability because of mostly PES-related biochemical traits driving decomposability and mostly SSS-related morphological traits driving flammability. However, their initial dataset suggesting support for this hypothesis was too small to be conclusive, while two other studies suggesting decoupling of decomposability and flammability, considered flammability of individual litter particles (Grootemaat et al., 2015; Grootemaat, Wright, van Bodegom, Cornelissen, et al., 2017), which are difficult to interpret in terms of field-relevant flammability of surface litter fuel beds. As oxygen limitation should be the most important driver for flammability when scaling up from single leaf to the surface litter fuel, testing this hypothesis at field-relevant litter bed level is needed (Ganteaume, 2018; Ganteaume et al., 2009, 2014; Scarff & Westoby, 2006).

Depending on the fuels consumed, natural fires can be classified into three types: crown, surface and ground fires (Bond & Keeley, 2005). In this study, we focus on the leaf litter on the soil surface, where interactions between decomposition and fire are the most important, while we do acknowledge the important contributions of standing live and dead biomass and soil organic matter to both processes (Cornwell et al., 2009; Grigulis et al., 2005; Mack et al., 2011; Popović et al., 2021; Stevens et al., 2020). But as the interface connecting crown and ground fire, the surface litter layer plays an important role in wildfire ignition and spread (Plucinski & Anderson, 2008) and vertically in starting most of the smouldering fires in organic soil or crown fires through fuel ladders (Blauw et al., 2017). Understanding how spectra of trait variation among surface litter fuels will affect relationships between fire and decomposition will help us to further understand the fire regime of the whole plant community. To our knowledge, we provide here the first comprehensive empirical test of the hypothesized decoupling of surface litter bed decomposability and flammability, and the underlying traits and trait spectra. We employ a species set of broad evolutionary spread, representing many of the important gymnosperm families and genera in the world, which are distributed in different habitats from fire prone to fire-free. Many gymnosperms often predominate in fire-prone habitats (especially in moderately cold and/or dry climate) both today and dating back to the Mesozoic (Belcher, Yearsley, et al., 2010; Miller, 1977). Their traits have had great impact on fire regimes in present and past (Belcher, Mander, et al., 2010; Cornwell et al., 2015; Schwilk & Caprio, 2011), and are likely to remain very important in the near future with warming climate and more frequent and intense drought periods (IPCC, 2021; Seidl et al., 2017). Thus, our group of gymnosperm species will help us test the hypothesis due to its variation in flammability and many of them have important roles in both past and current fire prone systems.

2 | MATERIALS AND METHODS

2.1 | Species selection and litter collection

We collected leaf litter from 41 gymnosperm plant species (Figure S1). To be able to include a wide range of higher taxa, all the leaf litters were collected from botanical gardens and tropical greenhouses in the Netherlands between 28 January 2011 and 2 March 2011: Pinetum Schovenhorst near Putten (52°15′N, 5°37′E), Pinetum Dennenhorst near Lunteren (52°05′N, 5°38′E), Pinetum Blijdestein in Hilversum (52°13′N, 5°09′E); Vrije Universiteit Amsterdam Hortus Botanicus (52°20′N, 4°51′E), Utrecht University Hortus Botanicus (52°09′N, 5°10′E), the greenhouse at Burger's Zoo (52°00′N, 5°89′E). The nomenclature follows The Plant List (2010). The phylogenetic tree was constructed by the R package V.PhyloMaker (Jin & Qian, 2019), which was implemented with a mega-tree derived primarily from Smith and Brown's (Smith & Brown, 2018) phylogeny for seed plants (i.e. GBOTB) and Zanne et al.'s (2014) phylogeny for pteridophytes. The plant material was collected as freshly seneced, that is, undecomposed litter. Many gymnosperm taxa drop foliated twigs instead of individual leaves (needles), and in such cases, we collected the litter in the configuration in which it was shed. The litter samples were air-dried and stored in open boxes in a temperature-controlled room in a laboratory at 21°C for 4–8 weeks until the fire experiment or trait measurements. Subsamples were stored in card-board boxes for the decomposition experiment.

2.2 | Trait measurements

Litter traits representing both PES and SSS were measured: carbon (C) content (PES), nitrogen (N) content (PES), lignin content (PES), pH (PES), lignin/N ratio (PES), litter tissue density (SSS&PES), packing ratio (SSS), litter particle volume (SSS), and shape index (SSS).

Leaf subsamples were oven-dried (48 h at 70°C) and ground to fine powder with a MM200 ball mill (Retsch). Then, carbon and nitrogen contents (%) were determined by dry combustion using a Flash EA 1112 elemental analyser (Thermo Scientific). Lignin content (%) was determined following to the method of Poorter and Villar (1997). The pH was measured according to Cornelissen et al. (2006). Litter tissue density (g/cm^3) was defined as oven-dried mass (70°C, at least 60 h) per litter volume. Litter volume (cm^3) was determined with a water replacement method (Williamson & Wiemann, 2010) after saturating air-dried subsamples in demineralized water for 24 h. For each burn, the litter bed volume was standardized using a steel mesh ring (25 cm in diameter, 3 cm in depth). Litter particles filled the ring in their natural configuration (samples composed of twigs or longer leaves were cut to lengths of approximately 7–10 cm when necessary before the fire experiments in order to fit in the fuel array), at a density representative of that observed in the field (de Magalhães & Schwilk, 2012; Plucinski, 2003). Packing ratio was determined as litter total volume per litter bed volume. Litter total volume was determined by total litter air-dried mass per ring, air-dried litter moisture content and litter tissue density. The moisture content of the air-dried litter particles was measured after oven-drying subsamples at 70°C for at least 48 h.

Litter particle volume (length × width × height; cm^3) was assessed by measuring the height, width and depth of leaves or foliated twigs of each species used in this experiment. In order to capture the average value of the particle volume, the structure of the smallest, medium and largest leaves or branch pieces were used, then mean values of length, width and height of the litter particle were calculated. In order to quantify the complexity of the litter particle shape, we made a scoring system in which each aspect contributing to the shape complexity of the litter particle (e.g. order of branching, leaf lobes, compoundness, petioles; see Figure S2) added to a cumulative score, which was defined as the shape index.

2.3 | Flammability measurements

For the experimental burns, we followed the method by van Altena et al. (2012). In brief, the standardized fire experiment was performed in the Fire Laboratory of Amsterdam for Research in Ecology (FLARE) located at Vrije Universiteit Amsterdam, the Netherlands. The leaf litter material was burned in a fire-proof ring of steel mesh (25 cm diameter, 3 cm depth), which was entirely filled with litter material of one species. The material was dropped into the ring evenly, allowing it to assume spontaneous configuration while at the same time being distributed equally over the ring, only applying very gentle pressure on the litter surface (to mimic slight compacting of the surface litter layer in the forest). Five replicates of all species were randomly placed in blocks, with one replicate per block. All replicates in each block were burned within a few days in the same week so as to provide similar air humidity in the fire lab within each block. During the burns, the temperature in the fire lab was 18 ± 2°C. The ventilation in the room was at a constant low speed. The ring was placed directly beneath the fume hood on a fire resistant plate. A cotton disc served as the ignition source. Before ignition, the cotton disc was soaked with 1 ml of 96% ethanol and placed in the middle of the ring, in a small pit in the fuel bed.

Ignition time (s), which represents ignitability, was measured with a stopwatch which represents the time for the first flames to appear from the litter after igniting the cotton wool. Maximum temperature (Tmax, °C), which represents the thermal energy released by the fire (intensity), was defined as the average of the maximum temperature of five thermocouples (1 mm thick type K thermocouple, TC Direct, Uxbridge UK) that were distributed evenly above the basket, with the tip of each thermocouple 12.5 cm from the centre and approximately 1 cm above the fuel surface. The proportion of sample burned, which represents consumability (indirectly representing the total heat or carbon loss during the fire), was defined as the mass loss fraction of the litter sample that was burned, based on the oven-dry weight of the sample before the burn and of the residue after cooling down. If a litter sample did not burn, or if the litter material only smouldered without the flames spreading, the sample was tagged as not prone to fire.

2.4 | Decomposability measurement

Litter decomposability was determined by performing a decomposition experiment in a 'common garden' litter-bed (Cornelissen, 1996). In October 2011, air-dried leaves (120–1800 mg according to the total amount of the collected leaves) of each species in this study were put in 1-mm mesh litterbags (10×10 cm^2, bags were cut to fit if less material; 3 replicates per species), then incubated outdoors in the Hortus Botanicus at Vrije Universiteit Amsterdam (52°20′N, 4°51′E) inside a litter layer on sandy soil. A flat area was first cleared of herbaceous surface vegetation and marked with a wooden frame (see Figure S3). Bulk mixed litter was collected from the soil surface in October 2011, combining a high proportion of freshly fallen *Taxodium distichum* litter (broad-leaved deciduous gymnosperm) from the Hortus Botanicus with mixed surface litter from a mixed woodland nearby (containing mostly *Quercus robur*, *Salix* spp., *Fraxinus excelsior*, *Betula pendula*, *Fagus sylvatica*) and horsetail (*Equisetum arvense*) and mixed grass litter from nearby (Figure S3). We assumed that this combination of litters, of broad taxonomic composition, would contain a diverse array of decomposers. After thorough mixing, a 3 cm layer of this matrix litter was spread out inside the frame as the incubation medium. The litterbags were spread out flat, without overlap, in random spatial species pattern (Figure S3), then covered with another 2 cm of the mixed litter. Large-mesh soft netting was stretched across the top of the litter bed to keep the litter matrix in position and prevent disturbance. The litter bed was left undisturbed until harvest of the litterbags after 12 months. Decomposition proportion was calculated as (initial litter oven-dry mass litter oven-dry mass after harvest)/initial litter oven-dry mass. Initial litter oven-dry mass was determined based on litter air-dried mass and air-dried litter moisture content of subsamples.

2.5 | Data analysis

All data analyses were processed in R (v4.0.3, R Core Team, 2020). Because of missing litter particle volume data, 4 species (*Ceratozamia mexicana*, *Dioon spinulosum*, *Encephalartos altensteinii*, *Encephalartos lehmannii*) were excluded from all particle volume related analyses. To interpret the variation in functional traits in terms of the intensity of phylogenetic signal, the *K*-value proposed by Blomberg et al. (2003) was calculated using the "phylosignal" function in the PICANTE package in R (Kembel et al., 2010). $K > 1$ indicates that functional traits exhibit a strong phylogenetic signal: $K < 1$ represents a weak phylogenetic signal. Linear regression was used to check the correlation between leaf litter decomposability and flammability, and the effect of litter traits (PES&SSS) on leaf litter decomposability and flammability. We additionally fitted our linear models using phylogenetic generalized least-squares regression analyses (PGLS) to correct for the effect of phylogenetic relatedness among species and nonindependence by using the phylogenetic tree constructed (Figure S1). PGLS analyses were conducted using the "pgls" function in the CAPER package in R (Orme et al., 2013). All data were $\log(x+1)$-transformed before fitting models.

A redundancy analysis (RDA) was carried out to reveal the relationships between decomposability and flammability parameters as constrained by the combined influences of various litter traits by the VEGAN package in R (Oksanen et al., 2019). Decomposability and flammability parameters were used as the respective response variables. Then, the response matrix was standardized by the decostand(method = 'normalize') function. The explanatory matrix was defined by the litter traits and $\log(x+1)$-transformed. Lignin/N ratio was excluded from the explanatory matrix to reduce collinearity (with Lignin and N content). For testing the significance of the variation in response matrix explained by explanatory variables, a Monte Carlo permutation test was used.

3 | RESULTS

The interspecific pattern of decomposition proportions was not correlated with any of the flammability parameters (ignition time, Tmax and proportion of sample burned; Figure 1). Most of the traits showed significant phylogenetic signals, as evidenced by Blomberg's *K* value (Table 1). All traits had weak phylogenetic signals ($K < 1$). The interspecific pattern of decomposition proportions was also not correlated with any of the flammability parameters with phylogenetic correction (Figure 1). The RDA results (Figure 2) also showed that the decomposability and flammability of leaf litter were decoupled across species. The leaf litter flammability parameters were strongly correlated with RDA axis 1, along with SSS-related traits. The decomposition rate of litter was strongly correlated with RDA axis 2 (Figure 2a), along with PES-related traits. Thus, RDA axis 1 could be considered as the flammability axis and RDA axis 2 as the decomposability axis. The species were distributed in all four quadrants (Figure 2b).

In the regression matrices without (Figure 3a) and with phylogenetic correction (Figure 3b), none of the four SSS traits (litter tissue density, shape index, packing ratio, and litter particle volume) showed any significant influence on leaf litter decomposition. However, most of the SSS traits had a significant influence on three flammability parameters, but differently for the two regression types. Shape index and packing ratio had no significant influence on ignition time in linear regression (Figure 3a), while their effects on ignition time became significant in PGLS (Figure 3b). Litter particle volume showed a significant influence on proportion of sample burned and Tmax with regular linear regression (Figure 3a), while its influence on both of these flammability parameters turned nonsignificant by PGLS (Figure 3b). Except N content, no PES trait showed a significant influence on the three flammability parameters, and the significant effect of N content on Tmax was no longer significant when analysed using PGLS (Figure 3). Lignin and C contents showed a significant negative influence on leaf litter decomposition (Figure 3). PES traits were partly significantly correlated with SSS traits, particularly lignin content with packing ratio (Figure 3).

The leaf litter shape index was strongly correlated with the litter particle volume (Figure 4a). The shape index was also significantly correlated with the packing ratio (Figure 4b). The litter particle volume was significantly correlated with the packing ratio by linear regression, but was only marginally significantly ($p = 0.053$) correlated with the packing ratio by PGLS (Figure 4c).

FIGURE 1 Relationships between decomposability (proportion of mass loss after 1 year) and three flammability parameters in litter layers: (a) Maximum temperature, (b) ignition time and (c) proportion of sample burned. *p* value and R^2 of linear regressions (*lm*) and phylogenetic generalized least squares regression (*pgls*) are given. All data were log($x + 1$)-transformed before fitting models.

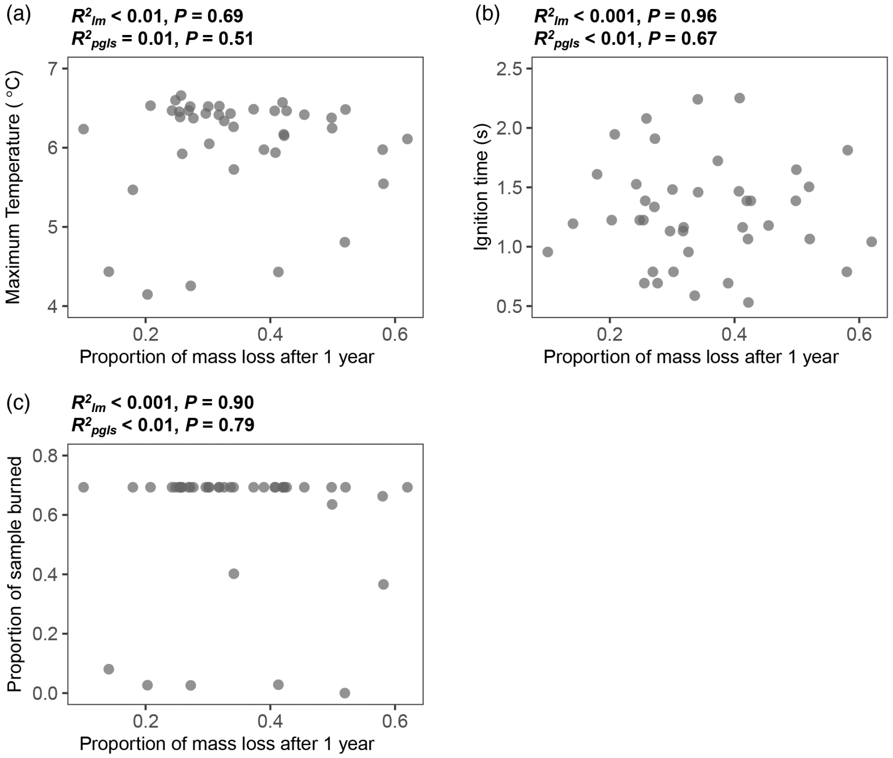

TABLE 1 The test of the phylogenetic signal (Blomberg's *K*) of all litter traits

	K	*p*
Maximum temperature (°C)	0.203	**0.008**
Ignition time (s)	0.150	**0.003**
Proportion of sample burned	0.342	**0.002**
1-year decomposition	0.050	0.546
Litter tissue density (g/cm^3)	0.185	**0.023**
Packing ratio	0.288	**0.001**
Litter particle volume (cm^3)	0.088	0.081
Shape index	0.379	**0.001**
pH	0.102	0.063
N (%)	0.064	0.286
C (%)	0.151	**0.005**
Lignin (%)	0.138	**0.008**
Lignin/N	0.062	0.399

Note: Bold font indicates a significant phylogenetic signal ($p < 0.05$). 1-year decomposition: Proportion of mass loss after 1 year.Abbreviations: C, Carbon content; N, Nitrogen content.

4 | DISCUSSION

4.1 | Are leaf decomposability and flammability decoupled across gymnosperm species?

Both (regular and phylogenetically corrected) regression and RDA results (Figures 1 and 2) showed that the decomposability and flammability of leaf litter were decoupled across species. The results of this large-scale analysis across gymnosperms are consistent with Grootemaat et al. (2015) and the preliminary findings by Cornelissen et al. (2017), which also suggested that leaf decomposability and flammability parameters are decoupled across species.

The species were distributed in all four quadrants representing scenarios of the trait combinations of SSS and PES (Figure 2b; see also Cornelissen et al., 2017): The dominance of species with high decomposability and low or high flammability (top two quadrants) could represent field scenarios in which fast decomposition leads to steady, moderate carbon release without sufficient fuel load accumulating to support a fire. Dominance of species of low decomposability and high flammability (bottom right quadrant) may represent a field scenario of high surface litter fuel load with good ventilation, that is, a potentially strong fire regime with episodic carbon release during dry periods. The predominance of species with low decomposability and low flammability (bottom left quadrant) could represent a scenario with high litter fuel load but poor ventilation, that is, a weak fire regime. This scenario would be consistent with a potential long-term carbon sink. Only very few species fall into this scenario. This would imply that our species selection may not include many of the species belonging to this scenario; or that species with low decomposability and low flammability generally have low fitness in surviving during the fire at the evolutionary scale. Fire may shape an ecosystem as an ecological and evolutionary driver, through flammability variations at the individual plant scale (Kane et al., 2022; Keeley et al., 2011; Pausas et al., 2017; Pausas & Moreira, 2012). The adaptive strategies of plant species in response to the fire regime would be to either evolve traits to resist fire (e.g. thick bark, resprouting), to escape from the fire (e.g. nonflammable strategy) or to

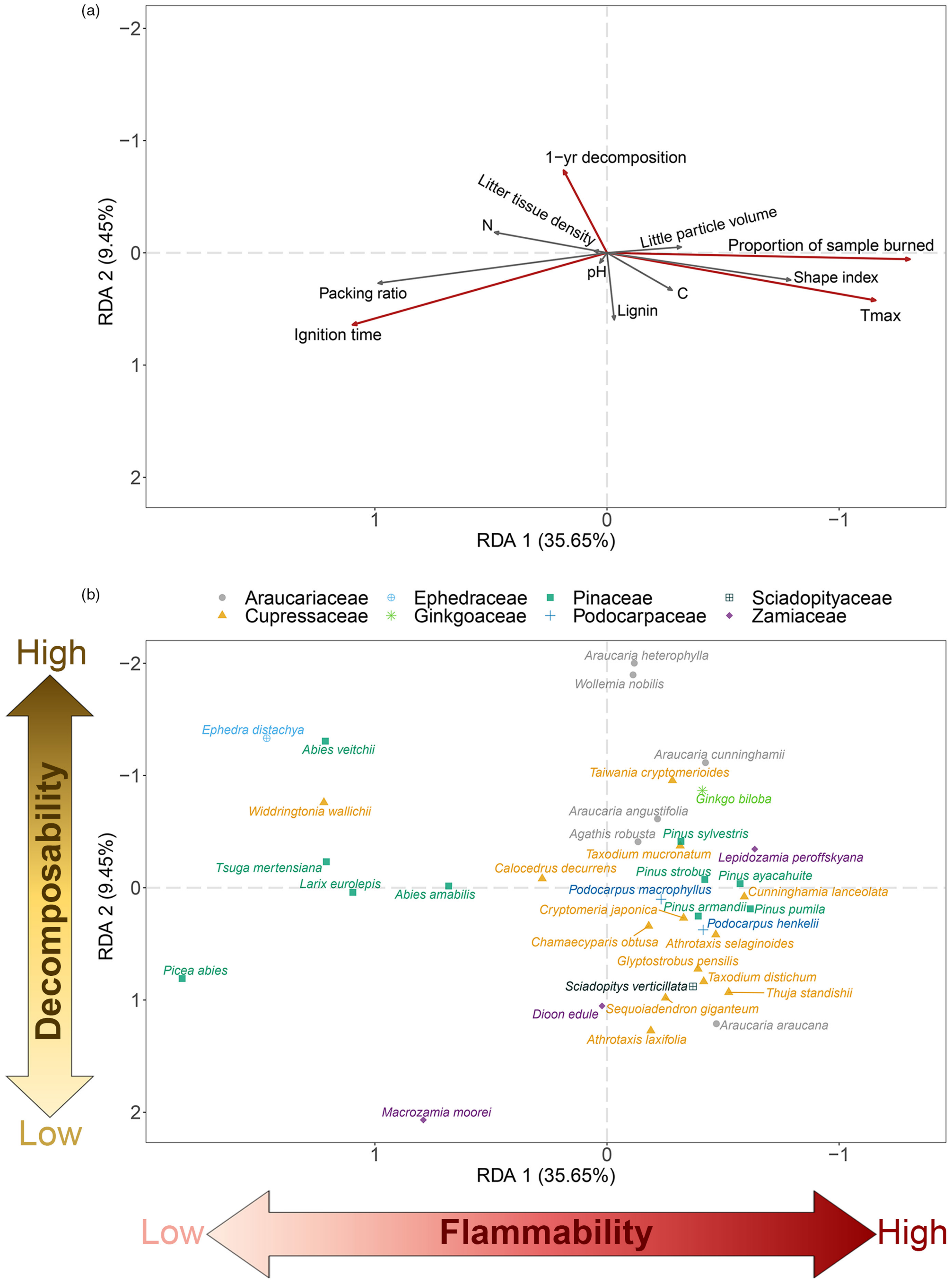

FIGURE 2 (a) Results of the redundancy analysis (RDA) for decomposability and flammability parameters in litter layers and leaf traits. (b) Distribution of gymnosperm species on the RDA1× RDA2 plane. The relationship is significant ($p < 0.01$) based on 999 permutations. 1-year decomposition: Proportion of mass loss after 1 year; N, Nitrogen content; C, Carbon content; Tmax, Maximum temperature.

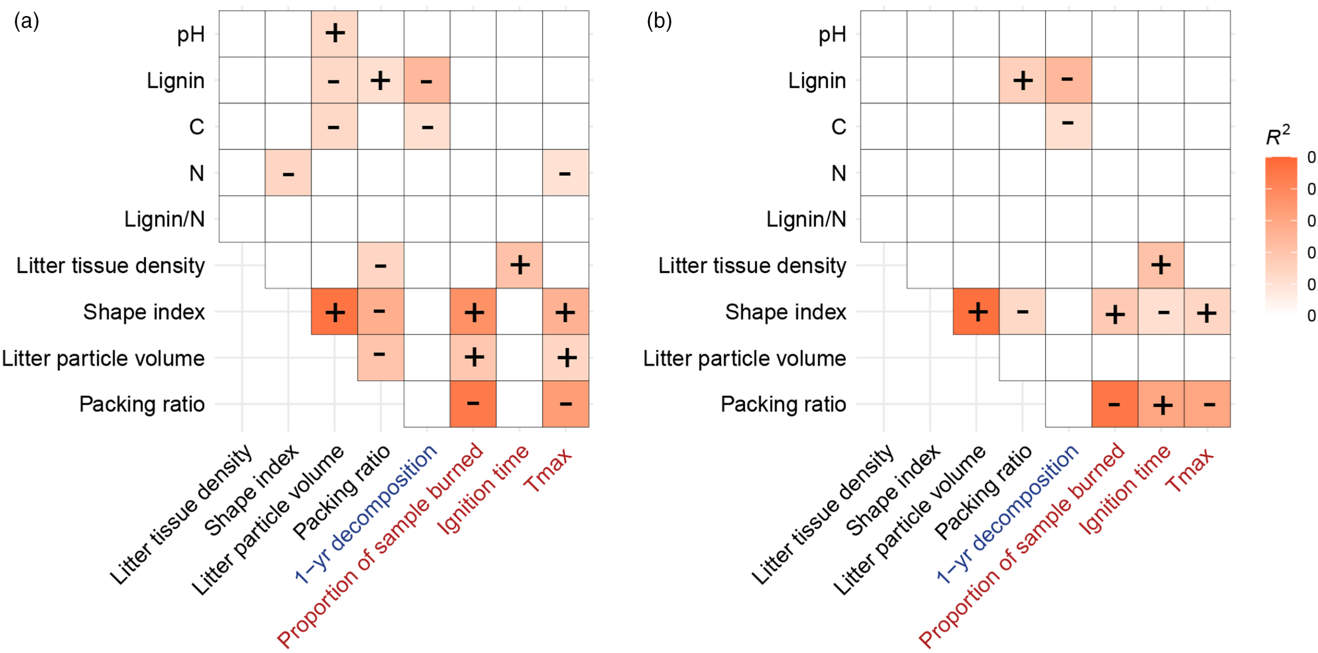

FIGURE 3 Regression matrices showing effects of different litter traits on decomposability and flammability parameters in litter layers: (a) linear regression result, (b) phylogenetic generalized least-squares regression result. The coloured cubes in the matrix represent the significant regressions ($p < 0.05$). 1-year decomposition: Proportion of mass loss after 1 year; N, Nitrogen content; C, Carbon content; Tmax, Maximum temperature. '+' indicates a positive and '–' a negative relationship between traits.

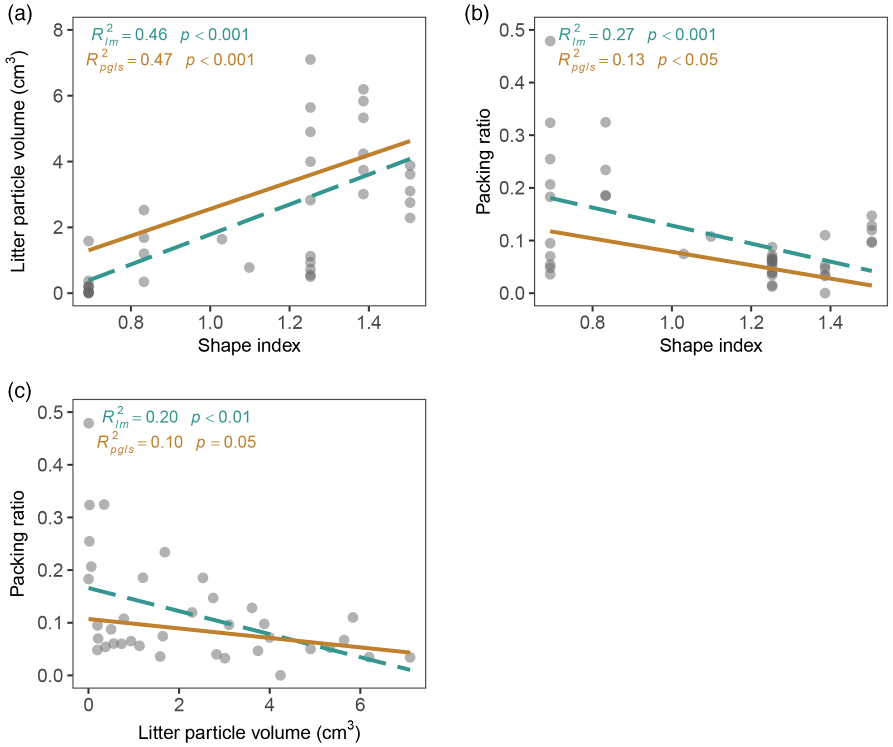

FIGURE 4 The relationship of (a) shape index with litter particle volume, (b) shape index with packing ratio and (c) litter particle volume with packing ratio. The dashed line indicates the result of linear regression (*lm*; green dash line) and the solid line indicates the result of phylogenetic generalized least-squares regression (*pgls*; brown line), R^2 and p value are given. All data were $\log(x + 1)$-transformed before fitting models.

quickly recruit after fire (e.g. post-fire seeders; Pausas et al., 2017). The top two quadrants with limited fuel loads would benefit tree species with fire resistant or fire escape strategies as surface fires rarely happen or hardly reach crown layers due to insufficient fuel load to sustain the fire. The bottom right quadrant would be most fit for the species with quick recruitment strategy. As for the bottom left quadrant with huge fuel load, even under poor ventilation and flammability, litter layers dominated by such species may still be susceptible to a major fire during extreme drought combined with strong wind (Falk et al., 2022; Pausas & Keeley, 2021). In other words, this scenario may only appear under certain climatic and environmental conditions. Species distributed at the low frequency fire regime are usually less fire resistant (Stevens et al., 2020). Thus for this scenario, infrequent but severe fires may have catastrophic impact on the whole plant community. This uncertainty for infrequent-severe fires may be the reason for the small number of species in this low decomposability-low flammability scenario.

4.2 | Decoupling of leaf litter decomposability and flammability explained by their different drivers in terms of PES and SSS traits

Our finding that leaf litter decomposability was generally decoupled from flammability (Figure 1), supports our expectation based on different traits underpinning decomposition and fire behaviour. On the one hand, interspecific variation in decomposition rate was not affected by any of the traits in SSS, and was mainly influenced by the carbon and lignin content (Figure 3), as in many previous studies (Aerts, 1997; Cadisch & Giller, 1997; Castellano et al., 2015; Freschet et al., 2012; Talbot et al., 2012). Indeed, lignin content belongs to the PES (Figure 3), as it has been linked with the trade-off between resource acquisition and resource conservation strategies of living plants (Freschet et al., 2010; Onoda et al., 2011). The recalcitrant, high lignin content litter could thus be an "afterlife legacy" of resource-conservative plants with long leaf lifespan (Cornelissen et al., 1999).

On the other hand, variation in the flammability parameters was generally strongly driven by traits belonging to the SSS (Figures 2a and 3). After phylogenetic correction, the effect of the litter particle volume on three flammability parameters became nonsignificant (Figure 3b). However, the shape index and packing ratio showed a significant influence on all flammability parameters (Figure 3b). In general, higher packing ratio significantly reduced litter flammability, as found in previous studies (Burton et al., 2021; Cornwell et al., 2015; Zhao et al., 2016). Among the chemical traits in the PES, only N content showed an influence on flammability parameters. However, no PES trait showed a significant influence on flammability parameters after phylogenetic correction (Figure 3b). Previous studies found evidence that some other biochemical traits (e.g. terpene content) are important for flammability at the litter bed scale (Dewhirst et al., 2020; Ormeño et al., 2009), and litter phosphorus (P) also has been shown to be a fire-retardant, although with low effect size (Grootemaat et al., 2015; Scarff & Westoby, 2008). However, the generally decoupled relationship between flammability and decomposability suggest that the influence of these chemical traits on flammability is still much less than that of SSS traits. Interestingly, the packing ratio was consistently positively albeit weakly correlated with the lignin content (Figure 3a,b). This may imply that the decoupling between the flammability and decomposability axis originated from the former depending mostly on SSS traits and the latter on PES traits and those trait spectra were virtually uncorrelated across species.

4.3 | The underlying drivers of packing ratio and its prediction

Interspecific variation in packing ratio, which was strongly linked with litter flammability at the litter bed level, was itself underpinned by litter shape and size at the litter bed level. While litter bed packing ratio could be seen as the emergent trait most directly representative of litter packing and, thereby, flammability in the field, its underlying traits are easily measured at individual litter particle level. Different from absolute litter volume as determined by the total volume of all tissues, litter particle volume in our study included the volume of litter itself and the space within the outer boundaries as created by its own structure. This made litter particle volume a trait that should well (negatively) predict packing ratio and the (negative) effect of packing ratio on flammability, as the nontissue air space within the boundaries of litter particle volume could be highly relevant for ventilation of the litter fuel bed.

However, the influence of litter particle volume on flammability was not significant after phylogenetic correction (Figure 3b), and its prediction of packing ratio was only marginally significant ($p = 0.053$; Figure 4c). This suggests that litter particle volume could not, solely, include most of the information provided by litter shape as a separate trait. While most previous studies only focused on the effects of leaf size-related traits (e.g. leaf curliness (uncorrected for leaf size), leaf length, leaf volume, specific leaf area) on flammability (Burton et al., 2021; Cornwell et al., 2015; de Magalhães & Schwilk, 2012; Engber & Varner, 2012; Ganteaume, 2018; Grootemaat, Wright, van Bodegom, & Cornelissen, 2017; Grootemaat, Wright, van Bodegom, Cornelissen, et al., 2017; Kane et al., 2021; Scarff & Westoby, 2006; Schwilk & Caprio, 2011; Zhao et al., 2016), leaf shape (index) was not really included before. Thus, we used shape index as the quantitative trait representing shape independently of litter tissue volume. According to the results, shape index showed better ability in predicting packing ratio compared with litter particle volume (Figure 4b). Additionally, the shape index had a stronger influence on litter flammability than litter particle volume (Figure 3). This suggests that the shape index could be an important trait of the SSS. However, our scoring system for shape index may still be fine-tuned by testing it also on different plant groups, for example across diverse angiosperms. With further improvement and expansion of the leaf shape database, this trait could become even more useful in predicting field litter bed packing and flammability.

4.4 | Limitations in our litter bed construction and the future complement in litter traits testing

In this study, the litter bed was built with single species under ideal environmental conditions for fire ignition and spread (i.e. dry and constant ventilation). We do acknowledge that this kind of lab experimental setup will bring artificial effects, which may not be fully representative of field litter bed conditions. In the real world, field environments will be more complex and vary greatly among geographical locations and ecosystems. Also, in the field situation leaf litter of different species and also dead leaves and twigs are often mixed, with possible nonadditive effects on flammability parameters (de Magalhães & Schwilk, 2012, 2021; Ganteaume et al., 2013, 2014; Zhao et al., 2016). Thus, our study is merely the first step to test the decoupled relation between decomposability and flammability of the surface leaf litter under simplified conditions. Testing the consistency of the hypothesis in field litter beds on a large scale under more complex environmental conditions (e.g. fuel moistures, wind speeds) will be needed. Additionally, as the surface fire is not the only natural fire type, investigating the linkages among the four scenarios in Figure 2 vertically with smouldering fire and crown fires through the traits of soil organic matter or standing live and dead fuels would be an interesting next step.

In this study, we mainly focused on PES traits that are linked with litter structure. However, other nutritional elements (e.g. P; see above) and large-chain organic compounds (secondary metabolites, e.g. tannins, flavonoids, resins and volatile oils) we did not measure in this study would have influences on both litter flammability and decomposability (Cornelissen et al., 2017). At litter bed level, according to our results and Cornelissen et al. (2017), we assume that the decoupled relationship of litter flammability and decomposability would still be valid under the full range test of PES-related traits, due to their small or inconsistent influences on litter bed flammability relative to SSS traits. Regardless, more experimental evidence from future studies including the full range of PES traits is required for fully understanding this decoupled relation.

In conclusion, this is the first study to comprehensively show that litter decomposability and litter bed flammability parameters are decoupled across a wide range of species. This decoupling originates from the former depending mostly on SSS traits and the latter on PES traits and those trait spectra being virtually uncorrelated. Scaling up from the experimental litter bed to complex field situations and including a full range test of PES traits will be important for more robust insight. Still, our empirical support for the hypothesized decoupling of litter layer decomposability and flammability represents a promising advance towards better understanding and predicting Earth surface carbon dynamics across biomes, while extension of the concept testing to diverse angiosperms will be an important next step.

AUTHOR CONTRIBUTIONS

William K. Cornwell, Weiwei Zhao, Richard S. P. van Logtestijn, Johannes H. C. Cornelissen and Eveline J. Krab carried out the experimental work. Shudong Zhang, Richard S. P. van Logtestijn and Johannes H. C. Cornelissen gathered the data. Shudong Zhang and Johannes H. C. Cornelissen analysed the data. Shudong Zhang and Johannes H. C. Cornelissen led the writing of the manuscript. All authors made important suggestions on at least two drafts of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

The authors do not have any conflict of interests to declare.

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DATA AVAILABILITY STATEMENT

Data are available at https://doi.org/10.5061/dryad.63xsj3v5n (Zhang et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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