Non-native plant legacies: site-dependent effects on deadwood fungal community species and functions

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Summary

1) The introduction of non-native species has consequences for ecosystem functions including deadwood decay. Non-native deadwood is a novel substrate for consumers, such as fungi, which drive large portions of carbon cycling, but their response to a novel substrate may depend on their local communities and surrounding environmental conditions.
2) We quantified decomposition rates, chemical composition and fungal communities of native and non-native deadwood across dry savanna and wet rainforest sites. We used six and five native angiosperm species in the rainforest and savanna, respectively as well as a non-native conifer in both.
3) Wood-dwelling fungal communities differed between sites and specific fungal clades showed different relative abundances in native versus non-native wood depending on the site. Non-native deadwood decayed slower than native deadwood with similar chemical properties in the rainforest but not in the savanna.
4) Our results suggest that depending on the environmental conditions in which non-native plants are introduced, the response of ecological communities and ecosystem

processes differ. Such effects could be further amplified as non-native introductions become invasive, including the spread of decay and disease, forms in which carbon and nutrients are released and/or function of important plant-fungal relationships.

Key words: Australia, deadwood, ecosystem function, fungi, invasions, non-native, *Pinus*, tropical

Introduction

The introduction of non-native plants has important repercussions for ecosystem functions, such as carbon (C) and nutrient cycling; decomposition of plant matter represents an important process of returning elements to the atmosphere or soil (Wijas *et al.*, 2024a). Studies on leaf litter decomposition found that non-native plants usually have higher decomposition rates than their native counterparts (Liao *et al.*, 2008; Ehrenfeld, 2010). The main reason why non-native plants tend to have increased decomposition rates is via the ecological strategy favouring fast growth creating leaves with lower C:nitrogen (N) ratios that decompose faster than leaves from native species (Ehrenfeld, 2010). However, this response may be context dependent based on the non-native plant species introduced (Castro-Díez *et al.*, 2014). For instance, coniferous species, which are non-native to many ecosystems around the globe (Nuñez *et al.*, 2017), are known to have low-quality litter for decomposers (Weedon *et al.*, 2009; Pietsch *et al.*, 2014).

While most decomposition studies focus on leaf litter, woody stems are another large plant biomass investment that generally decomposes slower than leaf litter (Pietsch *et al.*, 2014). Deadwood represents ~10% of C stocks in forests (Pan *et al.*, 2024; Wijas *et al.*, 2024a), and there is still large uncertainty as to the main drivers of its decay rates (Wijas *et al.*, 2024a). Three major components determine decay rates of wood: environmental conditions, wood construction including chemical properties, and decomposer communities (Wijas *et al.*, 2024a). Depending on the wood construction, which typically varies among species, and the environment in which plants are introduced, there may be large variations in their impacts on the decomposer community affecting decomposition.

Globally, microbes, especially fungi, are the most widespread decomposers of deadwood, with many species coexisting and competing for resources in a given piece of deadwood (Maynard *et al.*, 2018; Lee *et al.*, 2019). There are many uncertainties in how fungal community composition affects decomposition rates. In laboratory inoculation studies with a single deadwood and different fungal species, decomposition rates depended on the initial

fungal species that colonized the wood (Fukami *et al.*, 2010; Fukasawa & Matsukura, 2021). In nature though, such relationships are hard to disentangle as deadwood chemistry and fungal communities interact to influence decay rates (Lee *et al.*, 2022; Huang *et al.*, 2022; Yang *et al.*, 2024). For instance, deadwood decomposition is faster with higher N, phosphorus (P), and pH (Weedon *et al.*, 2009; Freschet *et al.*, 2012), as well as lower lignin especially as guaiacyl versus syringyl (Law *et al.*, 2023). Such influences can be independent of the fungal community in the deadwood (Lee *et al.*, 2022; Yang *et al.*, 2024). Ultimately however, the environment may be the most important driver of decay as it determines decomposer decay efficiencies; for instance, increasing temperatures lead to higher decay rates of wood (Zanne *et al.*, 2022). As we explore the consequences of non-native plant decomposition on ecosystem processes such as deadwood decay, it is important to understand the relative roles of wood chemistry, fungal community composition and environment in these novel systems.

Fungi are a diverse group of organisms, but those involved directly in the decay process of deadwood are mostly found within the Basidiomycetes and especially within the class *Agaricomycetes* (Li *et al.*, 2022). Other groups of fungi (e.g., *Ascomycetes*) that are not decayers may be found within wood as well. Species-specific chemical properties and environmental conditions of deadwood determine the colonisation and survival of wood-dwelling fungi (Krah *et al.*, 2018b; Purahong *et al.*, 2018, 2024; Fukasawa, 2021; Lepinay *et al.*, 2021; Brabcová *et al.*, 2022; Moll *et al.*, 2024). In particular, some fungi have host-specific adaptations to decay conifer over angiosperm wood (Krah *et al.*, 2018a). For instance, some classes of wood-decay fungi such as *Dacrymycetes* are more prone to decay conifers than angiosperms (Shirouzu *et al.*, 2012). Within the *Agaricomycyetes*, fungi from the families *Boletaceae* or *Gloephyllacea* are specialized to decay conifer wood while fungi from the *Agaricales* are specialised to decay angiosperm wood (Krah *et al.*, 2018a).

Species in the conifer genus *Pinus* are frequently used in plantations due to their commercial importance for many wood-derived products. *Pinus*, which are native to the Northern hemisphere, are frequently planted across the tropics and Southern hemisphere where they often become invasive (Payn *et al.*, 2015; Nuñez *et al.*, 2017) across habitats from dry grassy woodlands to wet temperate forests (Williams & Wardle, 2007). *Pinus* spp. have wood with different chemical properties compared to angiosperms that dominate in tropical regions, including lignin made solely of guaiacyl (Ralph *et al.*, 2019) that native fungi may not be adapted to decay, hindering their colonization and survival (Faix *et al.*, 1985; Cabral Almada *et al.*, 2021). In comparison, the wood of angiosperms contains a combination of both syringyl and guaiacyl forms of lignin, the former being more easily degradable.

Law *et al.* (2023) analysed wood decay at two sites along a moisture availability gradient (a dry savanna and a wet rainforest) in the Australian tropics and showed that non-native *P. radiata* had lower pH, N, P and syringyl:guaiacyl ratios and higher C compared to most angiosperm species at both sites (Law *et al.*, 2023). Due to lower water availability in savannas compared with rainforests, there were also lower fungal-mediated decay rates of deadwood (Law *et al.*, 2023; Wijas *et al.*, 2024b). Their work however did not test for differences in the fungal communities carrying out wood decay. Although very little is known about biogeographical patterns of wood-dwelling fungi, based on knowledge from soil fungi, deadwood should contain a higher proportion of *Agaricomycetes* and a lower proportion of *Sordariomyectes* in the savanna compared with the rainforest (Tedersoo *et al.*, 2014).

To understand the impact of a chemically novel non-native species on wood-dwelling fungal communities and deadwood decay rates, we extended the work of Law et al. (2023) to explore the role of wood-dwelling fungal communities in native versus non-native wood. For these studies, we ran an *in-situ* deadwood decay experiment with several native angiosperms and one non-native conifer (*Pinus radiata*) species over 3.5 years in savanna and rainforest ecosystems in tropical Australia. We hypothesized that *P. radiata* would harbour a different fungal community composition to deadwood from native angiosperm species, with for example more clades specialised for conifers. Law et al (2023) found that on average *P. radiata* decayed slower than most native species although it was unclear whether it was due to their chemical composition. Here, we hypothesized that the chemical properties of deadwood from *P. radiata* compared with those from native species would explain their lower decay rates. Finally, we hypothesized that different wood-dwelling fungi would dominate in the two sites.

Results

We found large variation in the composition of wood-dwelling fungal communities among deadwood from different species (Df_{93} = 11, χ^2 = 10.5, F = 2.9, P < 0.001), (Figure 1). As expected, there was little overlap in fungal communities at the OTU level between native species and *P. radiata* based on pairwise comparisons (Table S1). However, differences in relative abundances of fungal classes and families between native and *P. radiata* deadwood were site-dependent (Figure S1 and S2). For instance, at the class level, the proportion of *Agaricomycetes* was higher in deadwood from native species compared with *P. radiata* in the savanna but not in the rainforest (Figure S1). The proportion of *Dacrymycetes* was higher in deadwood from *P. radiata* compared with deadwood from native species in the

savanna. Contrary to our hypothesis, we did not find that conifer specialists within the *Agaricomycetes* class, such as *Boletaceae* or *Gloephyllacea* were more common on deadwood from *P. radiata* compared with native species (Figure S2).

In line with our hypothesis, deadwood in savanna had distinct fungal communities compared to deadwood in rainforest ecosystems ($Df_{93} = 1$, $\chi^2 = 4.2$, $F = 12.6$, $P < 0.001$), (Figure 1, Figure S3). We found that based on relative abundances, deadwood in the rainforest contained more fungi belonging to *Ascomycota,* particularly with more *Sordariomycetes* and *Eurotiomycetes* (Figure S3). However, we did not find differences in *Agaricomycetes*, although within this class, fungi belonging to the order *Agaricales* were more common in the rainforest while those belonging to the *Polyporales* were more common in savannas (Figure S3).

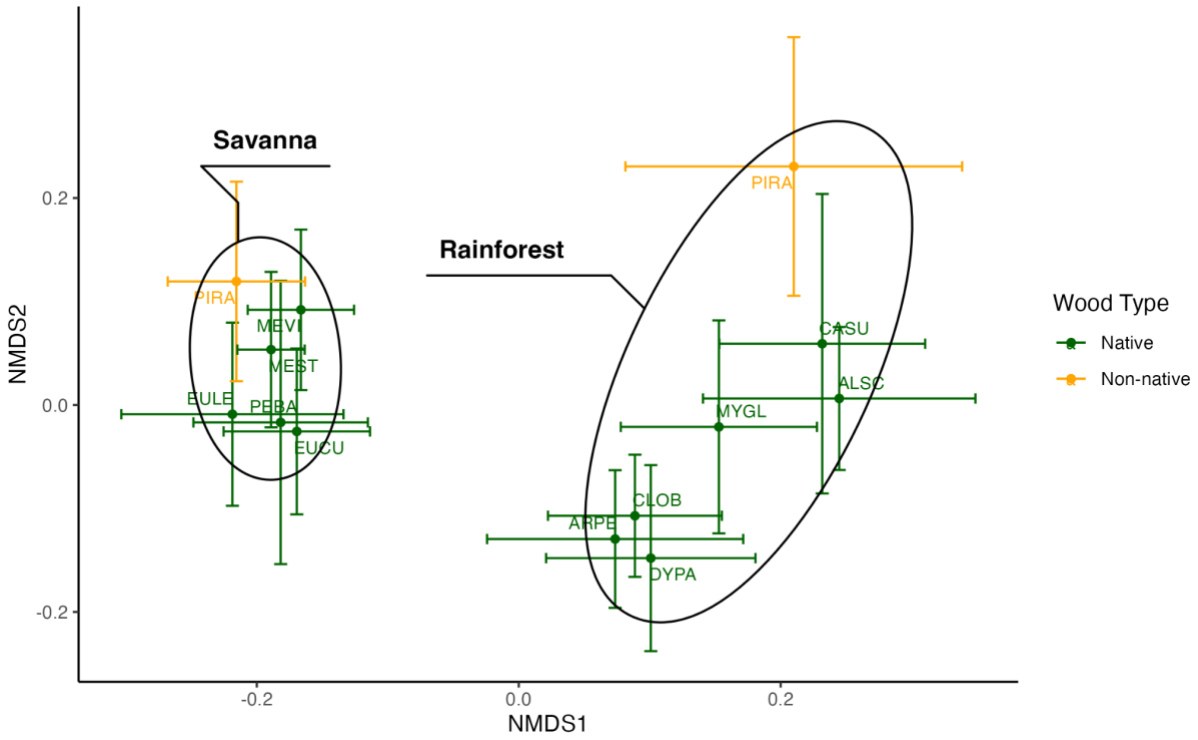

Figure 1 - Nonmetric multidimensional scaling of fungal communities using presence/absence of OTUs found with deadwood among 5 and 6 native species (green) in a savanna and rainforest, respectively, in addition to one non-native species (yellow). The abbreviations for each species correspond to the following - ALSC: *Alstonia scholaris*, ARPE: *Argyrodendron peralatum*, CASU: *Cardwelia sublimis*, CLOB: *Cleistanthus oblongifoloius*, DYPA: *Dysoxylum papuanum*, MYGL: *Myristica globosa*, EUCU: *Eucalyptus cullenii*, EULE: *Eucalyptus chlorophylla*, MEST: *Melaleuca stenostachya*, MEVI: *Melaleuca viridiflora*, PEBA: *Petalostigma banksii*, PIRA: *Pinus radiata*. The points represent the mean value for each species with error bars representing standard deviations.

Contrary to our expectation, *P. radiata* decayed slower than deadwood of similar chemistry in the rainforest as can be seen by the location of *P. radiata* on the PC2 axis of chemical wood properties (Figure 2). For instance, *P. radiata* deadwood decayed at almost half the speed of MYGL although they had a similar PC2. An increase in PC2 (mostly driven by a decrease in C) led to an increase in decay rates in the rainforest (*Estimate* (PC2) = 0.09, *Std. Error* = 0.03, *t-value* = 3, *p-value* = 0.04) but not the savanna (*Estimate* (PC2) = 0.02, *Std. Error* = 0.02, *t-value* = -0.79, *p-value* = 0.49), (Figure 2a). The difference in decay rates between *P. radiata* and native deadwood was less pronounced in the savanna where decay rates were on average lower than rainforest (*Estimate* (Savanna) = -0.18, *Std. Error* = 0.05, *t-value* = -3.91, *p-value* = 0.003). There was no relationship between decay rates of deadwood and PC1 in the rainforest (*Estimate* (PC1) = -0.06, *Std. Error* = 0.05, *t-value* = -1.27, *p-value* = 0.27) and savanna (*Estimate* (PC1) = -0.02, *Std. Error* = 0.03, *t-value* = -0.684, *p-value* = 0.54).

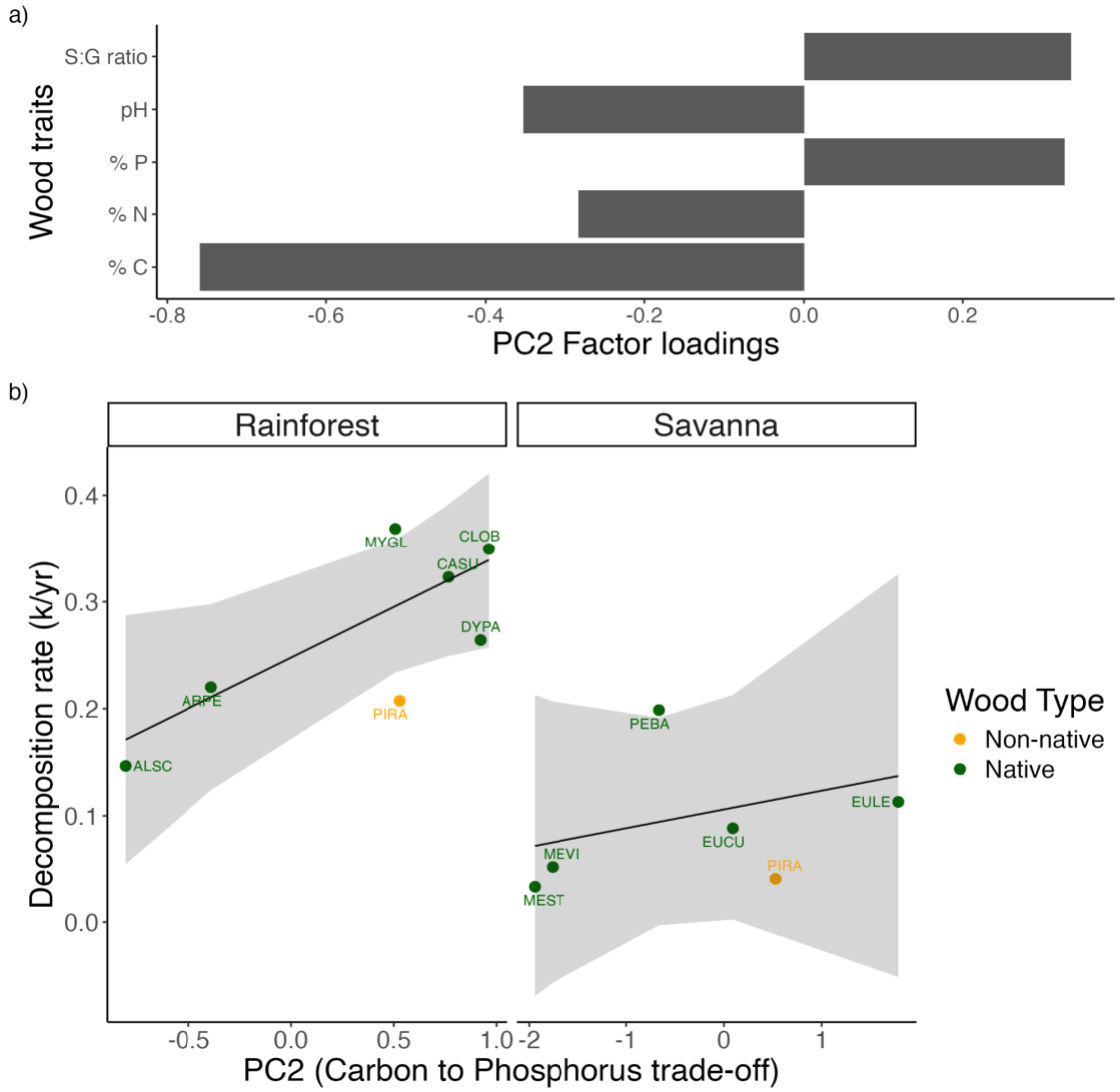

Figure 2 - a) Factor loadings of different deadwood traits (S:G = syringyl:guaiacyl, P = phosphorus, N = nitrogen, C = carbon) according to PC2 of deadwood chemical properties as shown in Figure S4. b) Decay rates (yr^{-1}) of deadwood from native (green) and non-native (yellow) species against the PC2 axis of chemical properties.

Discussion

Our results give insight into the mechanisms driving non-native plant impacts on ecosystems, as well as further implications as they become invasive. We found that the chemical novelty of deadwood from a non-native species may have acted as a filter on fungal community composition leading to different wood-dwelling fungal communities compared to those in deadwood from native species. However, there was site dependency in how fungal communities responded to the novel non-native substrates and how they decayed in comparison to chemically similar native species. Together, our results highlight the need to consider the broader environment in which non-native plants decompose,

especially regarding their chemical similarities with native species, to understand their repercussions on ecosystem communities and function.

Pinus radiata had a very different chemical composition compared with most native species at both sites, with a lower pH, syringyl:guaiacyl ratio, P and N as determined by PC1 of deadwood chemical properties (Figure S4). However, within PC2 chemical properties, which were mostly driven by C concentration, *P. radiata* deadwood had relatively similar chemical properties to native deadwood. The strong influence of PC2 rather than PC1 in determining decay rates in the rainforest site suggests that C content was the strongest driver of fungal decay capabilities in these ecosystems. These findings counter commonly assumed knowledge that nutrients are the main determinants of deadwood decay (Weedon *et al.*, 2009; Hu *et al.*, 2018) and highlight the need to carry out more deadwood decay experiments in tropical rainforests which are underrepresented in global datasets. *P. radiata* deadwood decay was slower than would be expected according to its C content in rainforests suggesting that other unmeasured novel chemical attributes or their different fungal communities may be leading to these differences. These may include the presence of resinous terpenes, lower percentage of living parenchymatous cells and the microscopic distribution of lignin (Weedon *et al.*, 2009).

While overall fungal communities significantly differed between *P. radiata* and native deadwood, we did not find evidence that known conifer specialists were especially enriched in *P. radiata*. Surprisingly, we found that the conifer specialist *Gloephyllacea* dominated in native deadwood in the savanna although it was rarely found in *P. radiata*. The other conifer specialist, *Boletaceae*, was rare across our sites explaining why these may not have been found in *P. radiata* either. It is important to note that for most native deadwood species in the rainforest, there were around 50% of fungal OTUs unassigned to the family level within the *Agaricomycetes*. Most knowledge on wood-dwelling fungal communities emanates from temperate ecosystems in the Northern hemisphere (Li *et al.*, 2022) although many plant invasions occur in the Southern hemisphere. Our results highlight an important knowledge gap that needs to be overcome to improve our understanding of consequences of plant invasions on fungal communities in the Southern hemisphere.

Despite such knowledge gaps, wood-dwelling fungal communities overall clearly responded to non-native deadwood differently between sites. Further, *P. radiata* deadwood decomposed slower than that of chemically similar native species in the rainforest but not in the savanna. These results highlight site-based context dependency in our understanding of non-native species' impacts on ecosystem community composition and function. For

instance, a stark contrast in fungal composition between *P. radiata* and native wood across sites is the replacement of *Agaricomycetes* by *Dacrymecetes* in the savanna but not the rainforests. While it is known that *Dacrymycetes* are more efficient decayers of *Pinus* over angiosperms (Shirouzu *et al.*, 2012), the surrounding environment in which these are found may influence their ability to colonise the wood. The drier environmental conditions and poor nutrient qualities of soils in Australian savannas may have led to plants constructing wood with ecological strategies more similar to conifer wood compared with native species from nearby rainforests (Law *et al.*, 2023; Flores-Moreno *et al.*, 2024). The microbial communities in the drier savanna such as *Dacrymycetes* may therefore be better adapted than those in rainforests to consume *P. radiata* due to their coevolution with the chemically similar but phylogenetically distant native species (Cornelissen *et al.*, 2023). Such results can be extended to think about the effect of non-natives as they become invaders in novel sites. A study by Ulyshen *et al.*, (2020) found site-dependent effects of plant invasions with larger differences in decay rates between non-native and native deadwood in sites where invasive plants were dominant. Together, our findings highlight a critical need for context dependency to be incorporated in future study designs to understand the impact of non-natives and invaders on ecosystem functions at micro (microbial) to landscape scales (Catford *et al.*, 2022).

Materials and Methods

Wood decay experiment

We set up our experiment in Far North Queensland, Australia, in a lowland rainforest at James Cook University's Daintree Rainforest Observatory (−16.1012°N, 145.4444°E) and in a dry savanna located in the Australia Wildlife Conservancy's Brooklyn Sanctuary (−16.5746°N, 144.9163°E). Mean temperatures were 24.4°C at the rainforest site and 24.7°C at the savanna site during the study period (https://power.larc.nasa.gov). The rainforest receives over four times as much rainfall as the savanna (rainforest: 4250 mm/yr from 1989 to 2019, weather station 31012; savanna: 960 mm/yr from 1989 to 2020, weather station 31180, https://www.bom.gov.au). Both sites have distinct wet and dry seasons with 80% and 94% of rain falling during November through April in the rainforest and savanna respectively. We note that while *P. radiata* is not currently invasive in our study sites, it and other species of *Pinus*, are common invaders in Australian ecosystems (Williams & Wardle, 2007).

We collected native wood stem sections from 6 rainforest species and 5 savanna species (Law *et al.*, 2023). There was no overlap in native species between the two sites. More detail can be found in Law *et al.* (2023) about species selection and experimental methods. Briefly, for each native wood stem, we harvested live stems from at least three individuals per species (ranging between 5-9 cm diameter) to a length of ~10 cm. The species were selected based on the relative abundance at each site, phylogenetic breadth and availability of stems. In addition, we obtained non-native *Pinus radiata* timber from a lumberyard in Cairns, Australia and cut it into 9cm x 5cm x 5cm wood blocks.

All native stems and non-native blocks were wrapped in 280um polyethylene Lumite mesh bags (Bioquip) to prevent access from invertebrates such as termites (Wijas *et al.*, 2024b). Additional stems and blocks were set aside to collect samples for initial wood chemistry. We obtained the dry mass of non-native wood blocks before setting those out in the field by placing them in a drying oven at 105ºC for 72h. To estimate the initial dry weight of each native stem on deployment, four other 'control' stems from the initial harvest of each species were weighed, dried at 105°C to constant mass, and reweighed. The dry weight of deployed stems was estimated by multiplying the fresh weight of the deployed stem by the mean fraction of dry weight calculated from control stems. The wood stems and blocks were placed out in June 2018. At each site, we set out 5 stations separated by 5m in which each wood block was separated by 15 cm to allow fungi to colonise the wood independently. We removed intact leaf litter from the ground before placing the blocks to assure that there was direct contact with the soil. In total, we deployed 5 stems or blocks for each species. Stems and blocks were allowed to decompose at each site until December 2021. After being collected, the wood blocks were brought back to the lab for processing.

To determine fungal community composition, we collected sawdust from each wood block following standard procedures (Powell *et al.*, 2021). The wood blocks were surface sterilised by submerging and rotating them first in 95% ethanol for 5 seconds, then in 0.5% sodium hypochlorite for 2 minutes and finally in 70% ethanol for 2 minutes after which they were air dried for >2 hours. Sawdust was obtained from >10 holes using a sterilised 3mm drill bit to a depth of 2.5 cm across all the surfaces of each stem and block. Sawdust was collected in tubes containing sterilised CTAB buffer. The tubes were stored at -80°C before further processing. After the sawdust was removed, the wood blocks and stems were dried at 105ºC for 72h and weighed to obtain a final mass value. We obtained decomposition rates for each species using mass loss through time and calculating k-values as detailed in Law *et al.* (2023).

Initial chemistry

To determine the initial chemistry of wood, we collected 5g of sawdust by homogenizing samples from 2 stems per species for native wood and 5 blocks for non-native wood using a 6 mm drill bit. The chemical components we measured included C, N and P content in addition to pH and syringyl:guaiacyl ratios. The specific methodologies for each of these tests can be found in Law *et al.* (2023).

Fungal community

To characterise fungal communities for each wood stem and block, DNA was extracted from 60 mg of sawdust using a modified CTAB DNA extraction protocol (Doyle & Doyle, 1987), as described in Powell et al. (2021). DNA samples were submitted to the Ramaciotti Centre for Genomics (University of New South Wales, Sydney, NSW, Australia). Fungal amplicons were generated using fITS7 (50-GTGARTCATCGAATCTTTG-30; (Ihrmark *et al.*, 2012)) and ITS4 (50-TCCTCCGCTTATT GATATGC-30; (White *et al.*, 1990)), purified using the Agencourt AMpure XP system (Beckman Coulter, Lane Cove, NSW, Australia), and genomic libraries were prepared with the use of the Nextera XT Index Kit (Illumina, San Diego, California, USA). Paired-end (2 x 251 bases) sequencing was performed on the Illumina MiSeq platform. To process the DNA sequencing data, we used the approach described by Bissett *et al.*, (2016) with a few modifications, as described in Nielsen *et al.*, (2024). Putative taxonomic identities for fungal OTUs were generated using BLAST (v.2.6.0, (Altschul *et al.*, 1990)) to compare representative sequences for each OTU to a reference database of gene sequences and taxonomic annotations (UNITE version 8.3, sh_general_release_dynamic_s_10.05.2021; (Abarenkov *et al.*, 2021)). Fungal ITS2 sequences were extracted using ITSx ((Bengtsson-Palme *et al.*, 2013), v1.1.3) for use during BLAST.

Analysis

We characterised fungal communities using non metric multidimensional scaling (NMDS) through the '*vegan'* package in R (Oksanen *et al.*, 2001). We calculated Sorensen distance based on presence or absence of fungal OTUs in each wood block and excluded OTUs which were found in <3 wood blocks. We used a PERMANOVA (>9999 permutations) with species and site as explanatory variables and then tested for pairwise differences in fungal community composition across different species of deadwood at each site. To determine which class of fungi and which family of fungi within the Agaricomycetes were driving

differences in community composition, we calculated the proportion of OTU reads belonging to each class or family for each wood block. For each class or family, we used generalised linear mixed effects models with proportion of reads as a response variable against the native status of the wood, site and their interaction as explanatory variables and applied a quasibinomial distribution given the proportional nature of the response variable. We used species as a random variable given that repeated measures were carried out on each species. To compare differences in community composition of fungi across sites, we applied a Wilcoxon rank sum test comparing the median relative abundance of each taxon between each site using the package *'metacoder'* (Foster *et al.*, 2017). We visualized these findings using a heat map tree.

Similarly to Law et al. (2023), we used a principal components analysis to assess the difference in initial chemical properties of native and non-native wood species by incorporating each chemical property we measured. To determine the role of initial chemistry in driving decomposition rates, we used the first two principal components for each species and ran a linear model with each principal component axis as an explanatory variable against decomposition rate within each site separately. This was due to the overwhelming difference in decomposition rates across sites.

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Competing interests

We declare no competing interests.

Author contributions

B.J.W. drafted the manuscript and carried out the data analysis with input from all co-authors. H.F. and A.E.Z. set up the experiment. J.R.P led the fungal sequencing. B.J.W, H.F, A.W.C, L.A.C and A.E.Z collected the data. S.D.A., H.F., L.A.C, A.E.Z and A.W.C contributed to experimental design. All authors edited and approved the manuscript.

Data availability

Data will be made available on Dryad upon acceptance.

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Supplemental materials

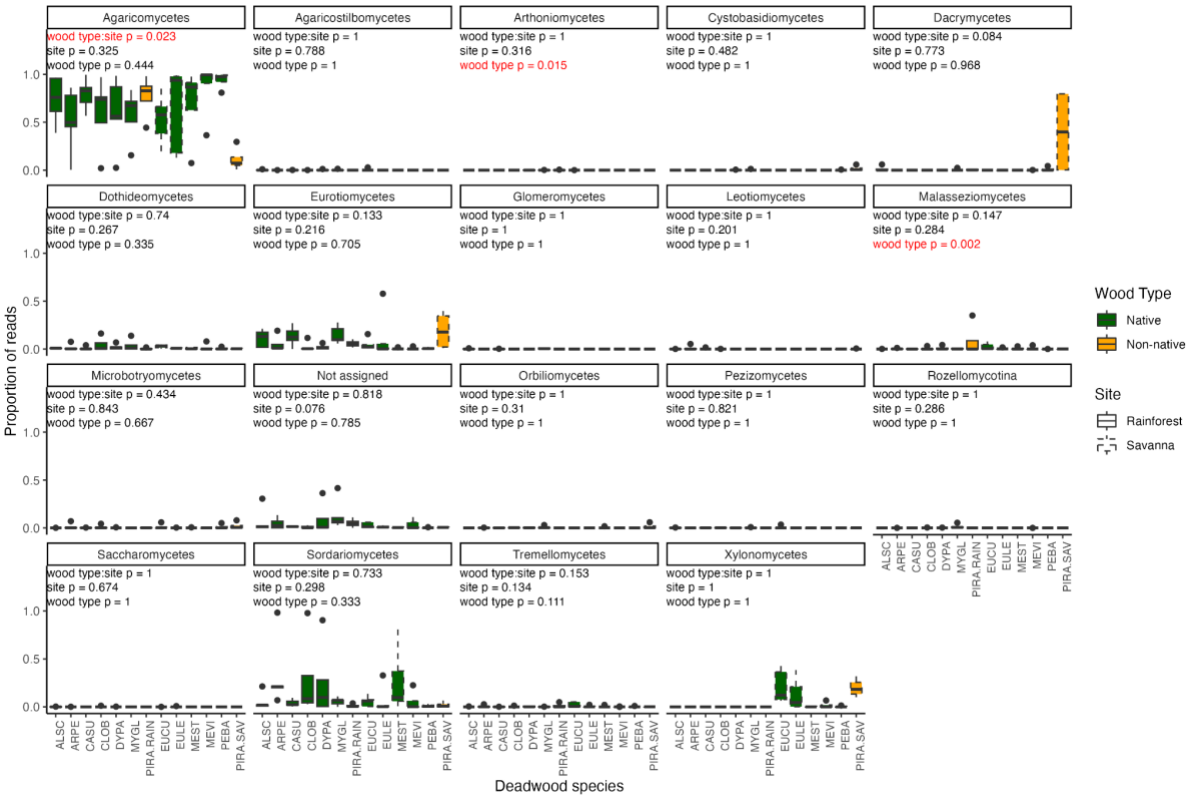

Figure S1 - Proportion of OTU reads belonging to each class of fungi across deadwood from native (green) and non-native (yellow) species in the rainforest (solid lines) and the savanna (dashed lines). The text above the boxplots represents the p-value for each explanatory variable from the linear mixed effects model with proportion of reads as a response variable against wood type, site and their interaction. Species was used as a random variable. P-values in red are significant (< 0.05).

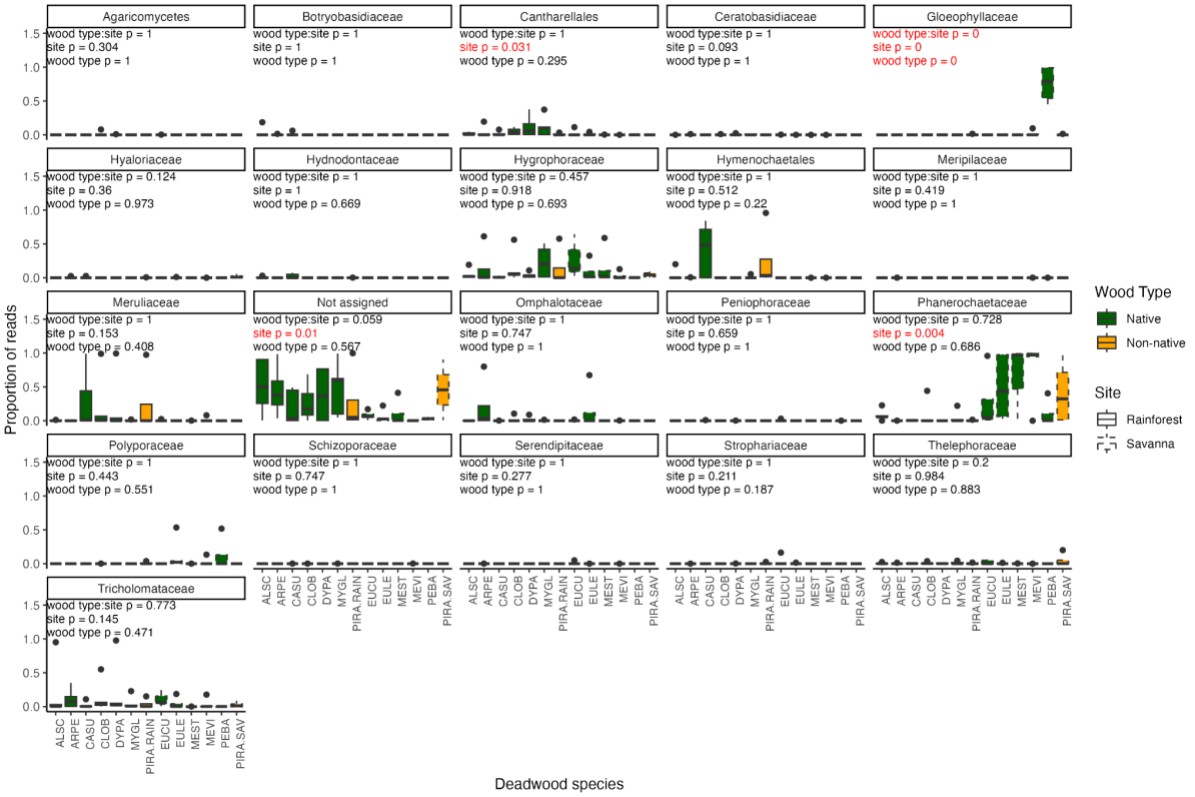

Figure S2 - Proportion of OTU reads belonging to each family within the *Agaricomycetes* across deadwood from native (green) and non-native (yellow) species in the rainforest (solid lines) and the savanna (dashed lines). The text above the boxplots represents the p-value for each explanatory variable from the linear mixed effects model with proportion of reads as a response variable against wood type, site and their interaction. Species was used as a random variable. P-values in red are significant (< 0.05).

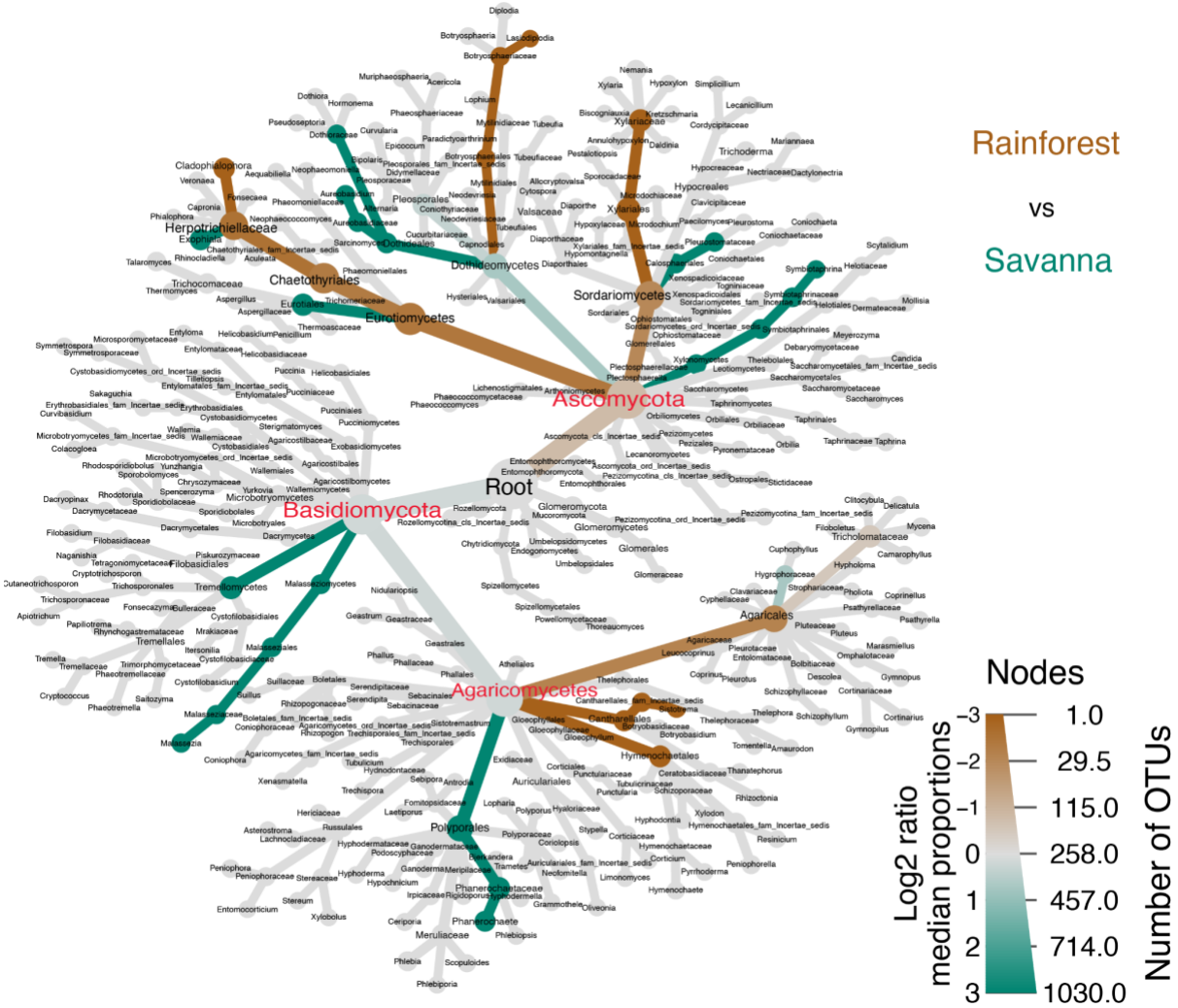

Figure S3 - Heat map tree representing differences in the relative abundance of fungi belonging to all taxa across sites with branches in brown representing those that are more common in the savanna and those in blue that are more common in the rainforest. The branch sizes represent the number of OTUs of each node.

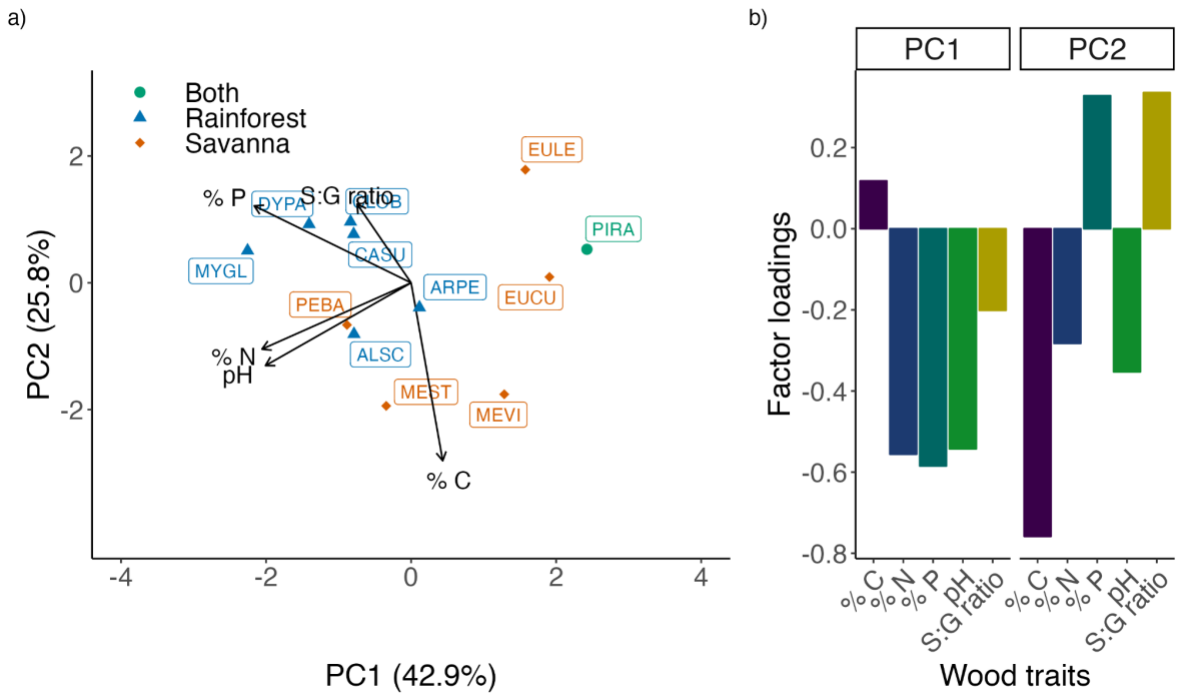

Figure S4 - a) Principal components analysis of deadwood chemical properties based on carbon (C), nitrogen (N) and phosphorus (P) content in addition to pH and syringyl to guaiacyl ratios (S:G). Each point represents a native deadwood species from the savanna (orange diamond), the rainforest (blue triangle) or a non-native species found in both (green dot). Each species has its accompanying label (ALSC: *Alstonia scholaris*, ARPE: *Argyrodendron peralatum*, CASU: *Cardwelia sublimis*, CLOB: *Cleistanthus oblongifoloius*, DYPA: *Dysoxylum papuanum*, MYGL: *Myristica globosa*, EUCU: *Eucalyptus cullenii*, EULE: *Eucalyptus chlorophylla*, MEST: *Melaleuca stenostachya*, MEVI: *Melaleuca viridiflora*, PEBA: *Petalostigma banksii*, PIRA: *Pinus radiata*). b) Factor loadings of the two principal components.

Table S1 - Pairwise comparison of fungal communities (presence/absence) among wood species. * Comparisons with *P. radiata*.

Site	*Pairs*	*Df*	*Sums Of Sqs*	*F.Model*	*R2*	*p-value*
Savanna	PIRA vs EUCU*	1	0.02	4.48	0.39	**0.02**
Savanna	PIRA vs EULE*	1	0.02	3.38	0.33	**0.04**
Savanna	PIRA vs MEST*	1	0.03	4.92	0.41	**0.01**
Savanna	PIRA vs MEVI*	1	0.02	2.95	0.30	**0.05**
Savanna	PIRA vs PEBA*	1	0.01	1.87	0.24	0.11
Savanna	EUCU vs EULE	1	0.00	0.53	0.06	0.93
Savanna	EUCU vs MEST	1	0.01	2.10	0.21	*0.07*
Savanna	EUCU vs MEVI	1	0.01	1.22	0.13	0.25
Savanna	EUCU vs PEBA	1	0.01	1.52	0.18	0.18
Savanna	EULE vs MEST	1	0.01	0.90	0.10	0.44
Savanna	EULE vs MEVI	1	0.00	0.62	0.07	0.60
Savanna	EULE vs PEBA	1	0.01	1.05	0.13	0.36
Savanna	MEST vs MEVI	1	0.00	0.70	0.08	0.66
Savanna	MEST vs PEBA	1	0.01	1.85	0.21	0.13
Savanna	MEVI vs PEBA	1	0.01	1.07	0.13	0.33
Rainforest	DYPA vs MYGL	1	0.01	2.65	0.25	**0.04**
Rainforest	DYPA vs CLOB	1	0.00	0.69	0.08	0.70
Rainforest	DYPA vs ALSC	1	0.01	3.62	0.31	**0.03**
Rainforest	DYPA vs ARPE	1	0.01	2.08	0.21	0.10
Rainforest	DYPA vs PIRA*	1	0.03	7.09	0.50	**0.03**
Rainforest	DYPA vs CASU	1	0.02	4.39	0.35	**0.03**
Rainforest	MYGL vs CLOB	1	0.01	2.46	0.24	**0.03**
Rainforest	MYGL vs ALSC	1	0.00	1.11	0.12	0.34
Rainforest	MYGL vs ARPE	1	0.01	2.91	0.27	**0.02**
Rainforest	MYGL vs PIRA*	1	0.02	5.29	0.43	**0.04**
Rainforest	MYGL vs CASU	1	0.00	1.11	0.12	0.37
Rainforest	CLOB vs ALSC	1	0.01	3.06	0.28	**0.01**
Rainforest	CLOB vs ARPE	1	0.01	2.02	0.20	*0.06*
Rainforest	CLOB vs PIRA*	1	0.03	7.53	0.52	**0.02**
Rainforest	CLOB vs CASU	1	0.02	4.01	0.33	**0.02**
Rainforest	ALSC vs ARPE	1	0.01	4.40	0.35	**0.01**
Rainforest	ALSC vs PIRA*	1	0.02	6.49	0.48	**0.01**
Rainforest	ALSC vs CASU	1	0.00	1.08	0.12	0.30
Rainforest	ARPE vs PIRA*	1	0.02	5.49	0.44	**0.01**
Rainforest	ARPE vs CASU	1	0.02	4.27	0.35	**0.02**
Rainforest	PIRA vs CASU*	1	0.02	4.76	0.40	**0.02**