

Forest fire may disrupt plant–microbial feedbacks

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Received: 16 January 2017 / Accepted: 15 February 2018 / Published online: 21 February 2018
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Abstract Plant–microbial feedbacks are important drivers of plant community structure and dynamics. These feedbacks are driven by the variable modification of soil microbial communities by different plant species. However, other factors besides plant species can influence soil communities and potentially interact with plant–microbial feedbacks. We tested for plant–microbial feedbacks in two *Eucalyptus* species, *E. globulus* and *E. obliqua*, and the influence of forest fire on these feedbacks. We collected soils from beneath mature trees of both species within native forest stands on the Forestier Peninsula, Tasmania, Australia, that had or had not been burnt by a recent forest fire. These soils were subsequently used to inoculate seedlings of

both species in a glasshouse experiment. We hypothesized that (i) eucalypt seedlings would respond differently to inoculation with conspecific versus heterospecific soils (i.e., exhibit plant–microbial feedbacks) and (ii) these feedbacks would be removed by forest fire. For each species, linear mixed effects models tested for differences in seedling survival and biomass in response to inoculation with conspecific versus heterospecific soils that had been collected from either unburnt or burnt stands. *Eucalyptus globulus* displayed a response consistent with a positive plant–microbial feedback, where seedlings performed better when inoculated with conspecific versus heterospecific soils. However, this effect was only present when seedlings were inoculated with unburnt soils, suggesting that fire removed the positive effect of *E. globulus* inoculum. These findings show that external environmental factors can interact with plant–microbial feedbacks, with possible implications for plant community structure and dynamics.

Communicated by Rogers.

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Keywords *Eucalyptus* · Forest fire · Plant–microbial feedback · Soil microbial communities · Soil inoculation

Introduction

Plant species may differentially modify soil microbial community structure through the addition of chemical

compounds and organic matter, thus altering habitat and resources (Ehrenfeld et al. 2005). These modified soil microbial communities may in turn affect the survival, phenology, or growth of plants via plant–microbial feedbacks (Bever et al. 1997). Plant–microbial feedbacks can have important landscape-level consequences for plant coexistence, diversity, and succession in temperate and tropical ecosystems (Johnson et al. 2012; McCarthy-Neumann and Kobe 2010a, b). In diverse tropical ecosystems, negative plant–microbial feedbacks are thought to maintain high levels of tree diversity (Mangan et al. 2010; McCarthy-Neumann and Kobe 2010a; Terborgh 2012). In these cases, the performance of conspecific seedlings is reduced in close proximity to adult trees due to an accumulation of host-specific soil pathogens, while the performance of heterospecific seedlings is relatively unhindered (i.e., a Janzen-Connell effect; Connell 1971; Janzen 1970). Plant–microbial feedbacks can also play an important role in plant community succession. For example, Kardol et al. (2006) observed negative feedbacks for early successional species, neutral feedbacks for mid-successional species, and positive feedbacks for late-successional species. However, little is known regarding the influence of external environmental factors on plant–microbial feedbacks.

While there is some evidence to suggest that soil type and nutrient availability may influence the sign and magnitude of feedbacks (Manning et al. 2008; Schradin and Cipollini 2012), the influence of forest fire is relatively unknown. Despite the obvious effects of forest fire (e.g., removal of aboveground vegetation and nutrient release), fire may also influence soil communities (Dooley and Treseder 2012; Xiang et al. 2014, 2015). This may occur directly through heat-induced mortality or indirectly via changes to soil physical and chemical properties (Dooley and Treseder 2012). As with plant–microbial feedbacks, these fire-induced changes to soil communities may also have consequences for plant performance (Allen et al. 2003, 2005; Soteris et al. 2013). For instance, Allen et al. (2005) found that the growth of six dry tropical tree species was generally improved with inoculation with mature forest as opposed to recently burnt forest soils. This suggests that forest fire may have a sterilizing effect on soil communities and disrupt plant–microbial feedbacks. With predicted increases in fire frequency under a rapidly changing climate

(McDowell et al. 2015), understanding how plant–microbial feedbacks are modified by forest fire will be important for predicting how forests might respond to these changing conditions.

The genus *Eucalyptus* is planted worldwide in forest plantations and is the dominant native genus of many Australian ecosystems (Williams and Woinarski 1997). The genus is of economic and ecological importance and, therefore, it is important to determine what factors drive the performance of these species. While there are some reports of eucalypt species differentially influencing soil chemical properties (Orozco-Aceves et al. 2015; Sayad et al. 2012), there is also evidence to suggest that eucalypt species can differentially modify soil communities. For instance, Anderson et al. (2013) found that *E. saligna* and *E. sideroxylon* seedlings modified distinct soil fungal communities after just five month's growth in a greenhouse experiment. *Eucalyptus* species are generally dependent on forest fire for establishment (Gill 1997). While fire is known to affect soil physical and chemical properties in eucalypt forests (see Certini 2005), it is also possible that fire may indirectly influence eucalypt growth via removing negative plant–microbial feedbacks that develop in forest stands.

Herein, we investigated whether two *Eucalyptus* species, *E. globulus* (subgenus *Symphyomyrtus*) and *E. obliqua* (subgenus *Eucalyptus*) display plant–microbial feedbacks and whether forest fire can remove these feedback effects. We collected soils from a native eucalypt forest on the Forestier Peninsula, Tasmania, Australia. Samples included soils collected from beneath mature *E. globulus* or *E. obliqua* trees within stands that had or had not been burnt by a recent forest fire. These samples were subsequently used to inoculate seedlings of both species in a fully factorial glasshouse experiment. We hypothesized that (i) eucalypt seedlings would respond differently to inoculation with conspecific versus heterospecific soils (i.e., exhibit plant–microbial feedbacks) and (ii) these feedbacks would be removed by forest fire.

Materials and methods

Soil collection

We sourced soil inoculum from a native eucalypt forest on the Forestier Peninsula in South-East

Tasmania, Australia (42°56'12.06"S, 147°53'40.92"E). The collection site was located in mature, 40–50-year-old damp eucalypt forest (up to 50 m tall) with an understory dominated by *Pomaderris apetala*, *Bedfordia salicina*, and *Olearia argophylla*. Soils were brown/red ferrosol derived from dolerite with moderately well-drained clay loams lying over medium to heavy clays; the area receives an average rainfall of approximately 900 mm per annum (Neyland et al. 1999). In January 2013 a wildfire burnt through the study area leaving a mosaic of burnt and unburnt stands. Within burnt stands, the understory and herbaceous layers were mostly removed and the lower trunks of mature eucalypts were burnt, but the fire did not reach the canopy.

One year following fire, we collected soils from six forest stands (detailed below) to use as inoculum in a glasshouse experiment testing for eucalypt plant–microbial feedbacks and the influence of fire on these feedbacks. To avoid any major changes in soil characteristics, the forest stands were located no more than 250 m away from one another. Soils were sampled from beneath mature *E. globulus* and *E. obliqua* trees (soil species) in stands that had or had not been burnt (burning treatment), giving four soil treatments (2 soil species × 2 burning treatments = 4 soil treatments). For each of these four soil treatments, soils were sampled from beneath ten trees in a mixed stand (codominated by both eucalypt species) and ten trees in a nearby pure stand (dominated by a single species), thus each soil treatment was represented by 20 soil samples. The identity of these 80 soil samples was retained throughout the experiment in order to have a robust error term to test for differences among the soil treatments. For each soil sample, the litter layer was removed and three soil cores (15 cm deep) were taken 1–2 m away from the tree (within the canopy and rooting zone) and then pooled. Soil samples were placed in a cooler immediately after sampling and the soil corer was washed with detergent and rinsed with water between each sample to limit cross-contamination of soils. Samples were then stored at 4 °C for no more than 48 h before being used to inoculate seedlings.

Preparation of plant material

Open-pollinated seed was collected from ten mature individuals of *E. globulus* and *E. obliqua* located

within 10 km of the site from where soils were collected. The seed collected from each individual tree was kept separate throughout the experiment and is hereafter referred to as a ‘family’. Seed capsules were dried at 40 °C for 72 h and sieved to collect seed. The seed of each family was germinated in sterile vermiculite in sterile plastic trays for three weeks until individuals of each species had developed their first pair of true leaves.

Plant–microbial feedback experiment

To test for the influence of fire on eucalypt-microbial feedbacks, we conducted a fully factorial glasshouse experiment testing the survival and growth responses of seedlings of each species to inoculation with each soil sample. The potting soil used consisted of eight parts composted pine bark and three parts coarse river sand with added macro- and micronutrients from Osmocote® for Natives low phosphorus, slow-release fertilizer (Scotts® Australia Pty Ltd, Baulkham Hills, NSW, Australia), which included N, Phosphorus (P), and Potassium (K) in the weight ratio of 19:2.6:10. Although this potting soil likely contained a basic soil microbial community, it was not sterilized because only steam sterilization and autoclaving were available. Both of these sterilization techniques can cause an increased growth response due to the release of nutrients from soils (Chen et al. 1991), particularly in soils with slow-release fertilizer as in the present case, and we suspected this would mask the effect of soil treatments. For each of the 80 soil samples, four sterile forestry tubes (200 ml) were three-quarters filled with potting soil. A small amount of soil sample (approximately 5% potting soil volume) was placed on the surface of all four forestry tubes to ensure that seedlings had first contact with the soil sample. Two of these forestry tubes were planted each with a single *E. globulus* seedling from the same family, while the other two forestry tubes were planted each with a single *E. obliqua* seedling from the same family. Each family was randomly allocated to eight *E. globulus* and eight *E. obliqua* soil samples. In the rare cases where insufficient seedlings were available, replacements from another family of the same species were used. With 80 soil samples planted with two seedlings from each of the two eucalypt species, the design consisted of a total of 320 forestry tubes. Forestry tubes were organized into a randomized block design,

where each combination of soil treatment and seedling species was represented twice in each of the 20 glasshouse blocks. Tubes with seedlings from the same family were generally assigned to different glasshouse blocks, and tube position within glasshouse blocks was assigned at random.

After 12 weeks of growth (before seedlings had become pot-bound) seedling survival was recorded and surviving seedlings were destructively harvested to test for the effects of inoculation with each soil treatment. Seedlings were carefully removed from their forestry tubes, with soil gently shaken and massaged off the roots. The roots were rinsed to wash off any remaining soil. Seedlings were cut at the root collar to yield above- and belowground biomass. The above- and belowground plant parts were placed in separate paper bags, dried at 60 °C for 48 h, and then weighed. The belowground biomass was divided by aboveground biomass to yield root to shoot ratio and both above- and belowground biomass were summed to yield total biomass.

Statistical analysis

All statistical analyses were conducted using the statistical package SAS (version 9.2, SAS Institute Inc., Cary USA). To test for plant–microbial feedbacks and the influence of fire, linear mixed effects models were fitted analyzing for differential survival and growth responses of *E. globulus* or *E. obliqua* seedlings to inoculation with each soil treatment using the GLIMMIX procedure. Biomass traits were analyzed assuming a Gaussian distribution of residuals, whereas survival was analyzed using a binomial model with a logit link function. Models were fitted separately for seedlings of each species and included the fixed terms of soil species (*E. globulus* vs. *E. obliqua*), burning treatment (unburnt versus burnt forest stands), and their interaction. Random terms in the model included glasshouse block ($n = 20$), family ($n = 10$), and soil sample within soil treatment ($n = 20$ per treatment). The latter random term was used to test the fixed effects using a Wald-type test with denominator degrees of freedom estimated with the default Containment method. The glasshouse block term was included to account for spatial variation within the glasshouse design and family was included to account for intraspecific variation within the seedling species. Plant–microbial feedback was indicated by a

significant effect of soil species (conspecific versus heterospecific soils) on the survival or biomass of a seedling species (Brinkman et al. 2010), while a significant interaction between soil species and burning indicated an influence of burning on plant–microbial feedback. As two seedling species were tested, significance levels were adjusted to $\alpha < 0.025$.

Residuals were tested for assumptions of normality and homoscedasticity for the biomass traits and appropriate transformations were applied to meet the Shapiro–Wilk test and diagnostic graphical representations were also checked. All biomass traits were log transformed.

To present feedback effects, the log-transformed ratio of response (Hedges et al. 1999) to inoculation with conspecific versus heterospecific soils collected from either burnt or unburnt soils was calculated for the total biomass of each species. Specifically, for each species, we took the logarithm of the averaged total biomass of seedlings when inoculated with conspecific soils divided by the average total biomass of seedlings inoculated with heterospecific soils (Brinkman et al. 2010). Response ratios were calculated from the least squares means of inoculum treatment groups obtained from mixed linear models (above).

Results

At the conclusion of the experiment, 91 and 64% of *E. globulus* and *E. obliqua* seedlings survived, respectively, but the survival of both species was not significantly influenced by soil species or burning treatment (Table 1). Although seedling survival was not supported by our first hypothesis, seedlings did display growth responses to soil species consistent with plant–microbial feedbacks. Above and belowground biomass responded similarly to the soil treatments (data not presented) and thus, we only report total biomass responses below. The *E. obliqua* seedlings did not show a significant response to the soil treatments. However, the total biomass of the surviving *E. globulus* seedlings was significantly influenced (adjusted $p = 0.004$) by an interaction between soil species and burning treatment. This interaction was driven by two significant pair-wise differences among soil treatments. Specifically, the total biomass of *E. globulus* seedlings was two-fold greater when inoculated with conspecific as opposed

Table 1 Results of linear mixed effects models that analyzed for the influence of the soil treatments on the survival and biomass traits of *E. globulus* or *E. obliqua* seedlings

	Surviving seedlings	Soil species		Burning treatment		Soil species × burning treatment	
		$F_{(1,53-68)}$	p	$F_{(1,53-68)}$	p	$F_{(1,53-68)}$	p
<i>E. obliqua</i>	102						
Survival		0.0	0.961	0.4	0.527	2.4	0.126
Total biomass		0.3	0.614	0.3	0.572	5.3	0.025
Root to shoot ratio		0.8	0.383	0.4	0.552	1.7	0.195
<i>E. globulus</i>	145						
Survival		0.3	0.565	0.0	0.853	1.0	0.311
Total biomass		0.5	0.469	2.4	0.125	10.2	0.002
Root to shoot ratio		0.2	0.640	2.1	0.155	0.1	0.823

For each test, the number of surviving seedlings at the conclusion of the experiment, numerator and denominator degrees of freedom, as well as the F and p values are reported. Bold values indicate statistical significance at $\alpha < 0.025$

to heterospecific soils collected from unburnt forest stands (adjusted $p = 0.014$), indicating a positive plant–microbial feedback. In support of our second hypothesis, the positive feedback effect exhibited by *E. globulus* seedlings was absent when inoculated with soils from burnt stands (Fig. 1), suggesting that forest fire modified soil microbial communities and removed

this feedback effect. Further, the total biomass of *E. globulus* seedlings was more than two-fold greater when grown in potting soil inoculated with unburnt conspecific as opposed to burnt conspecific soils (adjusted $p = 0.03$). The root to shoot ratio of both species was not significantly influenced by the soil treatments (Table 1).

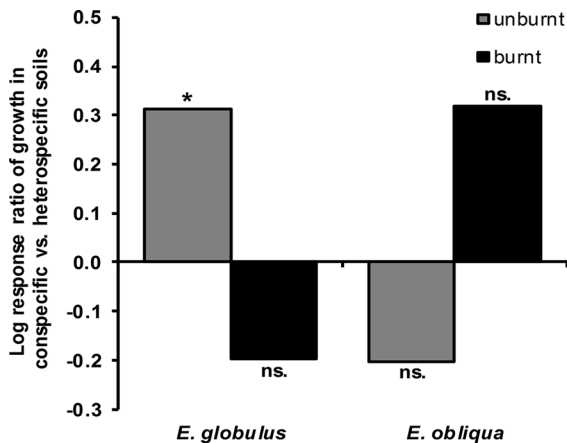


Fig. 1 Log response ratios of each eucalypt species inoculated with conspecific versus heterospecific soils collected from either unburnt or burnt forest stands. Response ratios are calculated from least squares means obtained from linear mixed effects models that analyzed for the effects of soil species, burning treatment, and their interaction on the total biomass of each species individually. The star above the *E. globulus* unburnt response ratio indicates a significant pair-wise contrast ($t_{66} = 2.8$, adjusted $p = 0.014$) between the total biomass of *E. globulus* seedlings inoculated with conspecific and heterospecific soils collected from unburnt stands

Discussion

Through inoculating eucalypt seedlings with fully factorial treatments of conspecific and heterospecific soils collected from burnt and unburnt native forest stands, three key findings emerge from this study. First, our findings suggest that eucalypt species may differentially modify soil microbial communities, as evident through seedling responses to inoculation with soils collected beneath two different eucalypt species. Seedling responses to inoculations were likely driven by soil microbes, as we only introduced a very small quantity of forest soils to forestry tubes (5% soil volume), thus any influence of soil chemical properties is unlikely. This method is often used in plant–microbial feedback studies, where soils are collected from known plant species in the field and used to inoculate seedlings in the glasshouse and test for feedback effects (Kulmatiski et al. 2008). Although the potting soil was not sterilized prior to the experiment, the fact that we observed soil treatment effects despite this implies that it was a true effect. For

this same reason, we are confident that the cleaning of field gear between samples with detergent limited cross-contamination. Second, eucalypt seedlings exhibited variable growth responses to inoculation with conspecific versus heterospecific soils consistent with plant–microbial feedback, but these responses were species-specific. We are only aware of a single study that has analyzed for plant–microbial feedback in *Eucalyptus* (Orozco-Aceves et al. 2015), where the authors detected no significant feedback effects. Third, despite the obvious removal of aboveground vegetation, forest fire appeared to modify soil microbial communities and interact with plant–microbial feedbacks. These findings indicate that plant–microbial feedbacks and external environmental factors, in this case forest fire, may interact to influence forest structure.

Our results suggest that eucalypt species may differentially modify soil microbial communities. While an observed effect of tree species on soil communities under field conditions may just reflect variation in the microhabitat occupied by the tree species, the fact that we sampled across eucalypt microhabitats within our site (i.e., mixed and pure stands), suggests that it was likely that eucalypt species modified soil microbial communities. Few studies have investigated whether eucalypt species modify distinct microbial communities (Anderson et al. 2013; Orozco-Aceves et al. 2015; Sayad et al. 2012). Yet, these studies support our findings by showing that eucalypt species may differentially modify both soil chemical and biotic characteristics, potentially through species varying in traits (i.e., growth rate and chemistry) related to the quantity and quality of organic matter entering soils (Baxendale et al. 2014; Orwin et al. 2010). In the case of our study, interspecific variation in foliar or root chemical traits (Li and Madden 1995; Senior et al. 2016) may have also contributed to differences in soil microbial communities, through influencing the quality of organic matter entering soils or by directly affecting root–microbe interactions.

Our findings suggest that species-specific effects of mature eucalypts on soil microbial communities can lead to plant–microbial feedbacks and that these feedbacks may vary among eucalypt species. We are only aware of a single study that has analyzed for plant–microbial feedback in *Eucalyptus*, where Orozco-Aceves et al. (2015) grew *E. marginata*

seedlings in field soils collected beneath *Pinus radiata*, *E. saligna*, and *E. marginata* trees. However, despite significant soil modification effects by the studied species, *E. marginata* displayed no significant feedback. We observed responses consistent with a positive plant–microbial feedback in *E. globulus*, where seedling performance was significantly enhanced when inoculated with conspecific as opposed to heterospecific soils. In contrast, *E. obliqua* seedlings displayed no significant plant–microbial feedback. The positive plant–microbial feedback exhibited by *E. globulus* may have been driven by mycorrhizae, as eucalypt species are known to form symbiotic relationships with both arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi (Adams et al. 2006). The fact that *E. obliqua* did not exhibit this feedback suggests that it may not share the same ability to form relationships with these organisms. Indeed, the two species included in this study belong to the two different subgenera occurring in Tasmania; *E. globulus* belongs to subgenus *Symphyomyrtus* and *E. obliqua* belongs to subgenus *Eucalyptus*. The two subgenera are known to differ in many ecological interactions, including their relationships with soil pathogens and mycorrhizae (Noble 1989; Podger and Batini 1971). Our findings indicate that the presence of plant–microbial feedbacks may vary among eucalypt species, possibly contributing to differences in their competitive interactions.

While fire is generally known to impact soil communities (e.g., Dooley and Treseder 2012; Xiang et al. 2014, 2015), to our knowledge, we are the first to investigate the influence of forest fire on plant–microbial feedbacks. A well-documented consequence of fire in eucalypt forest is the ‘ashbed effect’ (Humphreys and Lambert 1965; Loneragan and Loneragan 1964; Pryor 1963), where the germination and performance of eucalypt seedlings are enhanced following fire, particularly seedlings of species belonging to the ash group (subgenus *Eucalyptus*, series *Obliquae*; Ashton and Attiwill 1994; Neyland et al. 2009), which includes *E. obliqua*. The ashbed effect is thought to be mainly driven by fire-induced changes to soil physiochemical properties, but also may be in part driven by the sterilization of antagonistic soil microorganisms (Keeley and Fotheringham 2000). While we found no responses consistent with the sterilization of antagonistic soil microorganisms, our findings did suggest that fire may have sterilized

beneficial microorganisms. We observed responses consistent with a positive plant–microbial feedback in *E. globulus*, indicating an accumulation of beneficial microorganisms (e.g., mycorrhizal fungi) in the soils of adult trees that benefited the performance of offspring. However, we found this effect was absent in burnt stands, indicating that fire may disrupt plant–microbial feedbacks. Indeed, fire can influence both arbuscular mycorrhizal fungi and bacterial community composition, with effects lasting at least a year (Xiang et al. 2014, 2015). As most seedling recruitment in eucalypt forests occurs following fire (Gill 1997), this positive feedback effect may not be important during the early establishment of *E. globulus* seedlings in the wild, but could be during later growth. These findings raise the possibility that plant–microbial feedback and environmental factors may not act independently, but could interact, to influence plant community structure and dynamics.

Conclusions

Our findings suggest that soil microbial communities may vary at a local scale within native eucalypt forest and this variation is associated with both differing eucalypt species and patterns of forest fire. Further, this variation may in turn lead to species-specific feedback effects, potentially influencing the competitive interactions of species at establishment with lasting consequences for community structure. Lastly, the results of this study suggest that forest fire may disrupt plant–microbial feedbacks. However, to confirm these findings, future experiments are required to upscale this experiment across multiple sites as well as determine the mechanisms driving seedling responses to inoculation treatments. Specifically, next-generation sequencing could be used to confirm that different eucalypt species and fire modify microbial communities and identify specific microbial groups driving feedbacks. Our findings encourage further research into whether plant–microbial feedbacks and environmental factors interact as drivers of plant community structure and dynamics. Such research will be particularly important since disturbance events such as fire are predicted to become more frequent with global change (McDowell et al. 2015).

Acknowledgements We thank Hugh Fitzgerald for his assistance in the field as well as assisting with the planting, measurement, and harvesting the experiment. Thanks also to Michelle Lang for her expert advice in the glasshouse. Funding was provided by an Australian Research Council Discovery (Grant No: DP120102889).

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