Soils mediate the impact of fine woody debris on invasive and native grasses as whole trees are mechanically shredded into firebreaks in piñon-juniper woodlands

Zachary T. Aanderud [a, *], Donald R. Schoolmaster [b], Deborah Rigby [a], Jordon Bybee [a], Tayte Campbell [a], Bruce A. Roundy [a]

[a] Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602, USA
[b] US Geological Survey at National Wetlands Research Center, Lafayette, LA 70506, USA

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ABSTRACT

To stem wildfires, trees are being mechanically shredded into firebreaks with the resulting fine woody debris (FWD) potentially exerting immense control over soil and plants. We linked FWD-induced changes in microbial activity and nutrient availability to the frequency of *Bromus tectorum* and three native, perennial grasses across 31 piñon-juniper woodlands, UT, USA. Using a series of mixed models, we found that FWD increased the frequency of three of the four grasses by at least 12%. Deep, as opposed to shallow, soils mediated frequencies following FWD additions but only partially explained the variation in *Bromus* and *Pseudoroegneria spicata*. Although fertile areas associated with tree-islands elicited no response, FWD-induced increases in nitrogen mineralization in deep soils (15–17 cm) caused the frequency of the exotic and *Pseudoroegneria* to rise. Higher phosphorus availability in FWD-covered surface soils (0–2 cm) had no impact on grasses. FWD altered deep soil respiration, and deep and shallow microbial biomass structuring *Pseudoroegneria* frequencies, suggesting that microorganism themselves regulated *Pseudoroegneria*. The positive effects of FWD on grass frequencies intensified over time for natives but diminished for *Bromus*. Our results demonstrate that microorganisms in deeper soils helped mediate species-specific responses to disturbance both facilitating exotic invasion and promoting native establishment.

1. Introduction

Terrestrial environments are exposed to a diverse array of disturbances that alter ecosystem characteristics and induce microbial-mediated biological changes belowground. Disturbances that alter the quantity and quality of carbon (C) resources entering environments, in particular, have the potential to exert immense control over soil processes (Zechmeister-Boltenstern et al., 2015). Wildfires, tree-fall, typhoons and/or anthropogenic activities related to timber harvesting (Tinker and Knight, 2000; Murphy et al., 2008) result in the addition of dead and downed wood that promotes soil C storage (Klopatek, 2002), stimulates and depresses the fluxes of trace gases to the atmosphere (Hafner and Groffman,

2005), and releases new sources of energy for trophic web interactions (Norden et al., 2004). Further, many of the effects of woody debris on soils may extend aboveground.

Linking potential shifts in microbial activity to plant performance is extremely difficult, but clearer relationships may arise following disturbances. Disturbances often lead to dramatic shifts in aboveground plant community composition, especially when promoting the invasion and dominance of exotic species (MacDougall and Turkington, 2005). Following woody additions, the cover of exotic understory species increases in many forested ecosystems (e.g., tropical and coniferous forests; Kerns et al., 2006; Murphy et al., 2008) in part due to sunlight reaching the once-shaded understory as downed wood opens gaps in the overstory canopy. Woody additions may also alter the belowground environment and impact plants. In surface soils, woody additions generally lead to the immobilization of inorganic nitrogen (N) as microorganisms decompose copious recalcitrant wood substrates (Laiho and Prescott, 2004). However, in the absence of an overstory

* Corresponding author. Department of Plant and Wildlife Sciences, 4105 LSB, Provo, UT 84602, USA.
  E-mail address: zachary_aanderud@byu.edu (Z.T. Aanderud).

utilizing N, N may accumulate and be exploited by germinating and emerging seeds, and established understory plants. Deeper in soils, the resulting dead root system from canopy species may decompose and stimulate N mineralization and availability (Ehrenfeld et al., 1997) aiding in seedling recruitment. Besides N dynamics, dead and downed wood may alter other aspects of the soil environment favoring plant invasion. For example, woody debris may cause microorganisms to: 1) elevate soil water availability as decomposition and the production of extracellular polymeric substances modify surface debris and/or soil structure (Or et al., 2007; Young et al., 2013); 2) increase the release rates of essential plant macronutrients, such as phosphorus (P; Richardson and Simpson, 2011); and 3) change in abundance with species specializing in degrading woody substrates becoming dominant, and growth promoting rhizobacteria (Hayat et al., 2010) and mycorrhizae (Vandenkoornhuyse et al., 2003) becoming rare. However, the extent that these disturbance-induced shifts extend deeper into soils away from woody materials or translate into plant responses remains relatively unclear.

The action of shredding semi-arid trees, coupled with one of the most prolific plant invasions occurring in any ecosystem, offers an unprecedented opportunity to understand the links between fine woody debris (FWD)-induced changes belowground and native and exotic plant responses aboveground. The annual exotic grass, *Bromus tectorum* (L.), is a prolific invader that degrades piñon-juniper woodlands by replacing native grass species and creating monocultures of continuous fuels leading to catastrophic wildfires (Brooks et al., 2004). To stem wildfires and create firebreaks in piñon-juniper woodlands (Owen et al., 2009), thousands of hectares of trees are being mechanically shredded into FWD and translocated to the soil surface. Most FWD is being deposited in place on existing "tree-islands of fertility" in contrast to interspaces containing grasses, forbs, and biological soil crusts. The mosaics of islands of fertility and interspaces are chiefly responsible for differences in microbial activity prior to FWD additions (Aanderud et al., 2008) and may serve to augment the effects of FWD on belowground processes. Soils beneath trees are enriched with C and other essential elements (e.g., N, P, and calcium) due to roots acquiring nutrients from interspace soils and depositing them on the soil surface via litter inputs. Even under this enrichment, microbial activity in tree-islands is low due to the low quality of pine needle litter, and this limitation may be enhanced as more recalcitrant C sources from FWD are added to surfaces. Also, N transformations can be higher beneath tree-islands than interspace soils (Schade and Hobbie, 2005), and the addition of woody C sources, such as lignin, may only serve to immobilize N and reduce N release (Bates et al., 2002).

In this study, we evaluated the extent that soils mediated the responses of exotic and native grass species to FWD. In a replicated field experiment, where FWD was manipulated across 31 piñon-juniper woodlands, we linked FWD-induced changes in microbial activity and nutrient availability to shifts in the frequency of the invasive *B. tectorum* and three native, perennial grasses in the Great Basin Desert and Colorado Plateau, UT, USA. The three perennial species included: *Elymus elymoides* (Raf.) Swezey, *Poa secunda* (J. Presl), and *Pseudoroegneria spicata* (Pursh) Á. Löve. To understand the ecological consequences of a single disturbance type occurring at different times across 30 + ecosystems, we used a series of mixed models. Specifically, we developed models to: 1) describe the effects of shredding whole *Juniperus osteosperma* (Torr.) and the subsequent addition of FWD on N mineralization, P availability, microbial respiration rates, microbial biomass, and dissolved organic C (DOC) in surface and subsurface soils; and, 2) relate these changes to grass species distribution. We also examined these potential links across tree-island soils covered in FWD and relatively

bare interspace soils. The perennial grass species we selected are often influenced by *B. tectorum* invasions (Mangla et al., 2011) and represent dominant grasses in piñon-juniper woodlands. Thus, by examining these natives in tandem with *B. tectorum*, our results may offer a more comprehensive understanding into the consequences of shredding on species invasion. We hypothesized that: 1) the effects of FWD on shallow soils, immediately below the disturbance in particular, will explain some of the variation in the frequency of all grasses; 2) tree-island microsites will influence FWD-induced links between soils and grasses; and 3) changes in the availability of essential plant nutrients (i.e., N and P) and not microbial activity will be the prominent processes dictating grass response following FWD additions.

2. Materials and methods

2.1. Woodland sites

We conducted our study across 31 piñon-juniper woodland sites in the Great Basin Desert, Utah, USA. Dominant tree species included *Juniperus osteosperma*, and *Pinus edulis* (Engelm.) along with the shrubs *Artemisia tridentata* Nutt. (ssp. *wyomingensis* Beetle and Young, *tridentata*, and *vaseyana* [Rydb.] Beetle). We selected woodland sites with at least 15—45% tree cover estimated using images from the National Agricultural Imagery Program at 1 m spatial resolution (USDA-FSA-APFO Aerial Photography Field Office, Salt Lake City, UT). To ensure that the sites were indicative of semi-arid soil in the western USA, we measured the following physiochemical characteristics: pH from soil pastes (Thermo Orion pH meter model 410, Thermo Scientific Orion, Beverly, MA); electrical conductivity from 1:1 w/v extracts (Beckman Conductivity Bridge model RC-16C, Beckman Coulter Inc., Brea, CA); soil %C and %N with dry combustion on a C to N analyzer (LECO TruSpec CN Determinator, LECO Corporation, St. Joseph, MI); and soil texture (% sand, silt, and clay) with a hydrometer. Basic soils characteristics were based on three soil samples from a combination of at least one surface and subsurface soil sample to capture the overall environment at each site. The mean annual temperature and precipitation in woodlands was based on a thirty-year period (1982—2012) from PRISM climate datasets (http://www.prism.oregonstate.edu).

2.2. FWD manipulation and soil sampling

To investigate the effects of FWD on soils, we created three, randomly-selected FWD addition and three control plots (33 × 30 m) in each site. In the addition plots, whole *J. osteosperma* trees were shredded with a toothed drum (Cline et al., 2010), and the resulting woody material was deposited on the soil surface 1—8 years prior to sampling (2003—2010), which occurred over a 2-year period during the summer months (April—August 2011—2012). Our FWD fits best within the definition of fine down and deadwood employed by researchers in multiple other ecosystems (Norden et al., 2004; Muller-Using and Bartsch, 2009). Following whole-tree shredding, the dead and downed materials fall under the classification of FWD (diameter < 10 cm) and do contain classic FWD components (e.g., needles, twigs, small branches). These materials also consist of extremely woody components (e.g., logs and large branches) generally reserved for FWD (diameter > 10 cm; Muller-Using and Bartsch, 2009) that are only reduced in size but not different in chemistry. Specifically, the diameter of FWD ranged from 0.1 to 7.5 cm (Young et al., 2014) and FWD was piled on top of tree-islands.

To begin to understand the effects of FWD on links between soils and grasses, we sampled soils in *J. osteosperma* tree-island microsites at the surface (0—2 cm depth) where seeds may germinate and

emerge, and subsurface (15−17 cm depth) where establishing root systems may interact with nutrients and microorganisms. Roots of many dominant grasses in piñon-juniper woodlands, including our four study species, span these depths and are know to actively acquire resources from shallow and deep soils (James et al., 2008). The three microsite treatments included soils from interspaces (interspace), at the edge of the tree canopy or edge of woody addition piles (edge), and underneath the tree canopy or beneath the woody debris (canopy) approximately one-third the distance from the trunk of the tree to the canopy edge. In the FWD addition plots, microsites were identified using the shredded trunk of the shredded tree. We removed the soils from the three FWD addition and control plots with a corer (5 cm diameter × 10 cm length) and combined the three resulting subsamples from each treatment to create a composite sample for all microsite and depth combinations (2 treatments, FWD and control × 3 microsites × 2 depths × 31 study sites = 372 samples). The two depths were taken from different cores and were independent of each other. Soils were passed through a 2 mm sieve to remove rock fragments, stored at 4 °C, and used in soil laboratory incubations within 5 days of field sampling. To standardize sampling, we evaluated woody debris piles and standing trees with canopies approximately 3 m in diameter. Last, the FWD treatment and control plots were located as close to each other as possible within each site, with the maximum distance between plots no more than 2 km.

2.3. Grass species frequency

To identify grass species responses to FWD, we evaluated the frequencies of exotic *B. tectorum,* and three native perennial grasses *E. elymoides*, *P. secunda*, and *P. spicata* in tree-island microsites following debris additions. Specifically, we measured the occurrence of each grass across five randomly selected 30-m transects across each of the three FWD addition and control plots using the line-point method described by Roundy et al. (Roundy et al., 2014b; 2 treatments, FWD addition and control × 3 plots × 5 transects × 31 study sites = 930 transects). Using Python version 2.7.3 (Python Software Foundation, DE, http://www.python.org), first, we classified the 60 points along each transect into microsites (i.e., interspace, canopy edge, and tree canopy) based on the presence of tree canopies and woody debris. Second, we calculated the percent frequency of species as the number of times a species occurred in a given microsite divided by the total number of times that microsite occurred along each transect × 100. Third, we calculated the mean species frequency present for each microsite from the five transects in a given plot, and the mean species frequency in the three plots for the FWD and control treatments for each woodland.

2.4. Net N mineralization and P availability

We measured N transformation rates and estimated soil P availability to identify the influence of FWD on soil nutrients. In all soils, net N mineralization rates (mg N–NH_4^+ kg soil^{-1} day^{-1}) were measured as the change in NH_4^+ and NO_3^- in laboratory microcosms of surface and subsurface soils (Schaeffer et al., 2007). Microcosms consisted of 30 g of soil that was weighed into a specimen cup (155 mL), brought to a constant gravimetric water content (GWC) to simulate moist but not waterlogged conditions that semi-arid microorganisms may experience (0.3 g H_2O g dry soil^{-1}), and placed in a quart-sized Mason jar (volume = 935 mL). Jars had a gas-tight septum in the lid and contained 10 mL of water to keep samples from drying out during the incubation. Microcosms were incubated over 10 days at 30 °C. We measured NH_4^+ and NO_3^- at time zero and after 10 days in 0.5 M K_2SO_4 extractions (1:2 w/v) colorimetrically

(SpectraMax Plus 384, Molecular Devices Corporation, Sunnyside, CA). We used the methods outlined by James et al. (2008). for NH_4^+ and NO_3^-. An estimate of soil P (mg P kg soil^{-1}) availability was evaluated at time zero by extracting soils with 0.5 M NaHCO$_3$ (1:20 w/v) following the Olsen Sodium Bicarbonate method (Olsen et al., 1954) and measured colorimetrically.

2.5. Microbial biomass, soil respiration, and dissolved organic C

To evaluate the effects of FWD on microbial activity and potential links to grass frequencies, we evaluated microbial biomass, soil respiration, and DOC. Active soil microbial biomass (mg C kg soil^{-1}) was evaluated using a substrate-induced respiration (SIR) technique. Briefly, 10 g of soil was weighed into a specimen cup with a gas-tight septum in the lid (155 mL) and 1.1 mL of a 4.0 M sucrose solution was added to provide 4 mg sucrose g soil^{-1} and bring the soils to a constant GWC (0.3 g H_2O g dry soil^{-1}). We measured the difference between the initial and maximum respiration (24 h after sucrose addition) and calculated biomass using the equation: SMB (mg C kg soil^{-1}) = (40.04 × ΔCO_2) + 0.37 (Bailey et al., 2002), where ΔCO_2 is the change in respiration rates in units of μL CO_2 g^{-1} h^{-1} caused by the addition of the sucrose solution. We also measure soil respiration rates (mg CO_2 kg soil^{-1} day^{-1}) during the first 24 h in the same microcosms used to measure N mineralization. We extracted 10 mL of air from the microcosms with a 10 mL gas-tight syringe; measured CO_2 concentration (ppm) using an EGM-4 IRGA (PP Systems, Amesbury, MA), and converted CO_2 concentrations to mg, using the Ideal Gas Law. For DOC (mg C kg soil^{-1}), soils were extracted via a distilled water extraction (1:2 w/v), passed through a 0.45 μm nylon filter, and measured on a TOC-N analyzer (Shimadzu, Columbia, MD).

2.6. Model set 1: FWD and soil characteristics

We evaluated links between FWD-induced changes in microbial activity and nutrient availability to shifts in grass frequency with a series of mixed models to account for site as a random effect (Bolker et al., 2009). First, we created models estimating the effect of FWD additions on five soil characteristics in shallow and deep soils with the *lmer* function of the lme4 package (Bates et al., 2014) in R (R core team, 2015). Models were of the form,

$$y_i \sim N\left(\alpha_{j[i]} + \sum_k \beta_k x_{ki}, \sigma_y^2 \right) \tag{1}$$

and included site location, *j*, as a random effect, $\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2)$, and tree-island microsites as a covariate, *x*. All soil data used as inputs into the models were based on differences between FWD and control treatments by woodland sites and allowed for the inclusion of time since FWD addition as a covariate. While using this differencing method, if there was no effect of FWD treatment on a measured response (i.e., y$_{FWD}$ = y$_{control}$), then the response variable y' = log$_{10}$ (y$_{FWD}$) − log$_{10}$ (y$_{control}$) = 0. Alternatively, values of y' > 0 indicated that FWD caused an increase relative to the control, and y' < 0 indicated that the FWD treatment caused a decrease compared to the control. For the model, we estimated the effects of FWD on soils as model intercepts and determined significant differences based on 95% confidence intervals. Thus, a significant effect of the FWD treatment was indicated if the confidence interval of the intercept did not include zero.

2.7. Model set 2: The effects of FWD on grasses and the potential mediation of soils

Next, we fit a second set of models, one for each species

estimating the total effect of FWD additions on the change in grass frequency as a function of all five soil characteristics from both depths representing hypothesized explanatory variables. We followed logic of tests of mediation (Shrout and Bolger, 2002). Three possible meaningful outcomes identifying the effects of FWD on links between species frequencies and soil characteristics were possible (Fig. 1). The outcomes included: 1) the effects of FWD on species frequencies were entirely mediated through changes in soil variables due to woody additions (Fig. 1a); 2) the effects of FWD on species frequencies were partially explained by FWD and soil variables independently, suggesting that other unmeasured effects of the FWD treatment impacted species frequencies as well (Fig. 1b); and 3) the FWD treatment alone explained the variation in grass frequencies (Fig. 1c). We estimated the potential for soils to mediate this relationship by comparing the change in intercepts between grass frequency models including and excluding soil variables. If belowground characteristics explained any of the variation in grass frequencies, then the intercept from the model, including soil variables, should be closer to zero than the intercept from the model excluding soil variables. Further, the 95% confidence intervals should also decrease in size from models that exclude to those that include soil variables. As with the first model, these models were based on FWD and control treatments by woodland sites with time since FWD addition as a covariate difference and site location as a random effect. For more explanation of the logic test, equations, and modeling process see Supplemental Model Explanation (Supplemental Materials).

2.8. Model set 3: Links between FWD-induced changes in soils and grasses

Last, we generated a third set of mixed models, similar to the second set, one for each grass species to suggest specific links between FWD-induced changes in individual soil variables and grass frequencies. The resulting links between model parameters can roughly be interpreted as the percent change in the response variable given a 1% change in the explanatory variable. All models used the same differenced data, covariates, and random effects. The *p*-values for the effects of soil variables on grass frequency were calculated using likelihood ratio tests with the *lmer* function of the lme4 package in R. The magnitude and directionality of links were identified between soils and grasses and all models were combined into one figure to help interpret differences among grass species. For more explanation of the mixed models see Supplemental Model Explanation (Supplemental Materials).
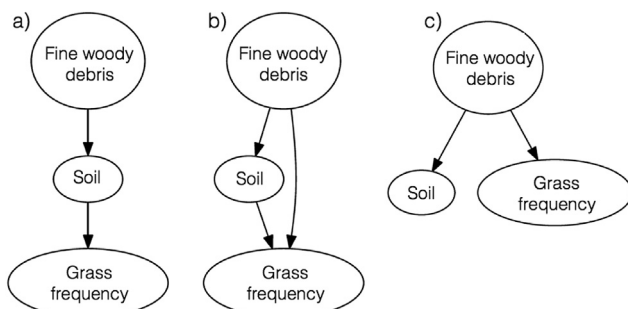
Fig. 1. Three possible outcomes from logical mediation tests identifying the effects of FWD on links between species frequencies and soil characteristics. The tests included: 1) the effect of FWD on species frequencies was mediated through changes in soil variables due to woody additions, 2) both the FWD treatment and the effects of woody additions on soil variables partially mediated the variation in species frequencies, and 3) the FWD treatment alone explained the variation in grass frequencies.

3. Results

3.1. Woodland site characteristics

Soils were sandy to clay loams with neutral pH and low salt concentrations, but varied in total % C and % N. Across the 31 woodland sites, soil texture was dominated by sand (mean and ±standard error of the mean (SEM), 45% ± 2.5) and silt (32% ± 1.5; Supplemental Table 1). All woodland soils possessed a neutral pH (7.0 ± 0.08) and low non-saline ECs (0.64 ± 0.06 dS m^{-1}). The % C varied from 0.63 (±0.05) to 9.4 (±2.2) and total % N varied from 0.08 (±0.01) to 0.26 (±0.05). Sites experienced mesic temperatures with mean annual temperatures of 9.7 °C ± 0.27, and a semi-arid climate with mean annual precipitation of 366 mm ± 10. The elevation of the sites ranged from 1637 to 2298 m.a.s.l. (Supplemental Table 1).

3.2. Model set 1: FWD influenced P availability, DOC, and C mineralization
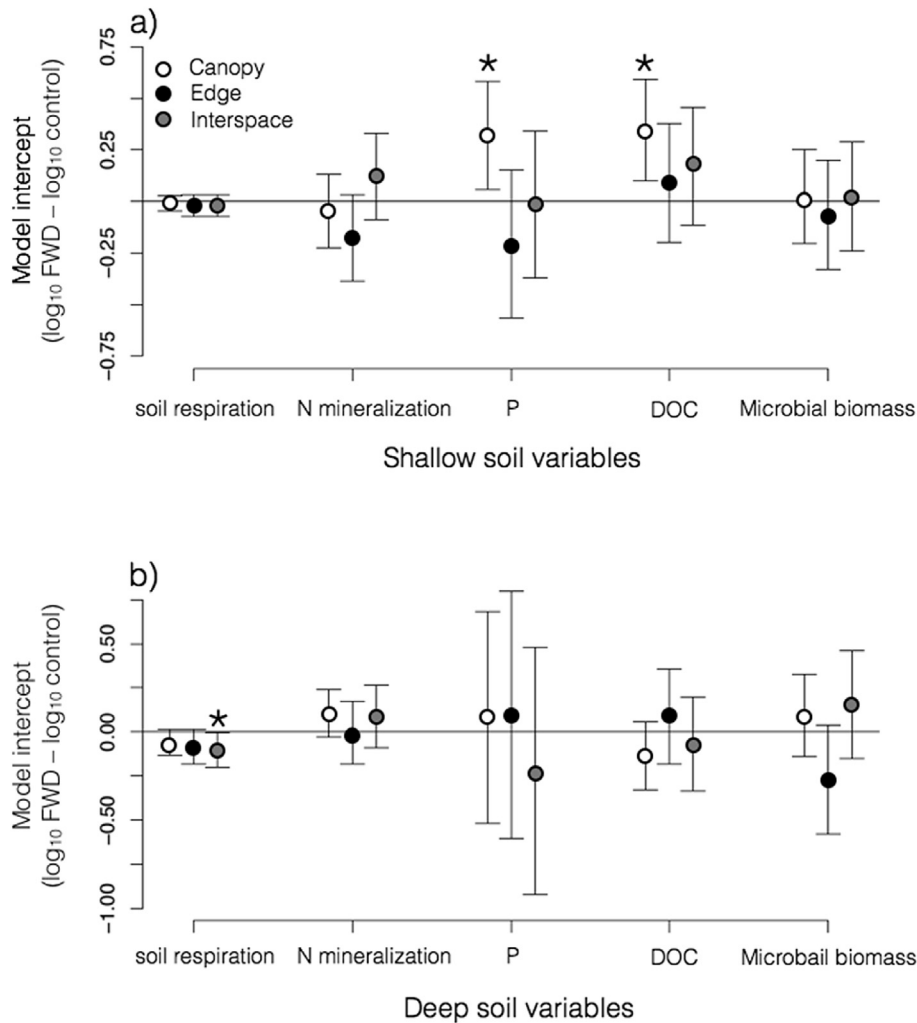
The addition of FWD stimulated soil P availability and DOC in canopy surface soils and depressed microbial activity in deep interspace soils (Fig. 2). Woody debris increased the availability of P at least 2.2-fold in canopy compared to interspace and edge soils (95% confidence interval of the intercept did not include zero). The addition of FWD also elevated the concentration of DOC, but only in canopy soils. As for activity, C mineralization was 4.2% and 9.5% lower in deep interspace than edge and canopy soils respectively. For means and ±SEM from the FWD and control treatments, see Supplemental Table 2.

3.3. Model set 2: Soils mediated the effects of FWD on exotic and native grasses

The addition of FWD influenced the frequency of *B. tectorum*, and two of the three native perennial grasses, *P. spicata* and *E. elymoides*, but soils only mediated the frequencies of *B. tectorum* and *P. spicata*. Based on the intercepts estimating the experimental effect of FWD additions alone (models including woodland sites as a random effect and time since FWD addition as a covariate, i.e., designated as site in Fig. 3), FWD increased the frequency of the exotic by 14% and the natives by at least 12% (Fig. 3a, c, 3d). Alternatively, *P. secunda* was not sensitive to FWD, because its 95% confidence interval overlapped zero (Fig. 3b). Further, due to the reduction in intercept between the two models excluding and including soil variables (i.e., site versus site + soil, Fig. 3), the effects of FWD on soil characteristics reduced or explained 25% and 41% of the variation in *B. tectorum* and *P. spicata* frequencies, respectively (Fig. 3a and c). Thus, the exotic and native followed the second outcome from the logic tests with both FWD and the effects of woody additions on soil variables partially mediating their frequencies. Alternatively, the inclusion of the effect of FWD on soils actually increased the uncertainty in predicting the frequency of *E. elymoides*, because the intercept increased following the inclusion of soils (Fig. 3d). Thus, *E. elymoides* followed the third outcome and its frequency was entirely influenced by FWD not mediated by soils. Including time since shredding as a covariate reduced the variation in intercepts and was retained in the models. However, the inclusion of tree-island microsites into the models did not explain any of the variation in grass frequencies or improve the fit of any model and was dropped as a covariate.

3.4. Model set 3: Specific links between FWD-induced changes in soils and grasses

FWD-induced changes in microbial activity in deeper soils, (i.e.,

Fig. 2. Fine woody debris (FWD) additions stimulated soil phosphorus (P) availability and dissolved organic carbon (DOC) in canopy surface soils, but depressed soil respiration in deep interspace soils. Microsite treatments included soils in barren plant interspaces (interspace), at the edge of the tree canopy or edge of FWD piles (edge), and underneath the tree canopy or beneath FWD (canopy). Values are intercepts, μ_α, with attending 95% confidence intervals from mixed models estimating the effects of FWD on five soil characteristics. Significant variables are indicated with an asterisk (i.e., 95% confidence interval of the intercept did not include zero). All data used in the model were based on differences between FWD and control treatments by woodland location ($n = 31$).

soil respiration, net N mineralization, and microbial biomass) and P availability in shallow soils, influenced the exotic and two perennial grasses. Although, FWD additions influenced only soil respiration, P availability, and DOC within tree-island microsites (Fig. 2), when microsite was dropped from the model, two new FWD-driven changes were evident (Fig. 4). These links were implied due to the detection of significant effects of N mineralization and microbial biomass on *B. tectorum* and *P. spicata* responses. Specifically, N mineralization significantly influenced the frequency of *B. tectorum* ($p = 0.02$) and *P. spicata* ($p = 0.01$) following FWD additions. Based on the mixed models, a 1% change in N mineralization induced the frequency of *B. tectorum* and *P. spicata* to increase by 0.36% and 0.23% respectively. Also, microbial biomass in deep soils marginally depressed the frequency of *P. spicata* ($p = 0.07$), while biomass in shallow soils marginally stimulated this same species ($p = 0.06$). In deep soils, FWD reduced soil respiration, and this reduction resulted in a marginal decline in *P. spicata* ($p = 0.07$), indicating a positive relationship or linkage between this soil variable and grass. The availability of P in shallow soils influenced one native, but unlike N mineralization, the increase in P availability following FWD additions actually negatively impacted *P. secunda*. Overall, the

frequency of this native grass was insensitive to FWD, but soils with higher P availability reduced *P. secunda* ($p = 0.03$) frequency. Although not statistically significant itself, the intercept for time since shredding was negative for *B. tectorum* (-0.15, $p = 0.17$) and positive for both perennials, *P. spicata* (0.17, $p = 0.20$) and *P. secunda* (0.17, $p = 0.16$), demonstrating significant links to soil processes.

4. Discussion

The effects of woody debris on ecosystems are often highlighted in coniferous and deciduous temperate forests where debris may constitute a substantial portion of total C and strongly regulate ecosystem processes (Pregitzer and Euskirchen, 2004). Recently, however, there is an unparalleled addition of woody debris occurring in piñon-juniper woodlands for which there is no ecological precedent. The management practice of shredding piñon-juniper trees has often aided in the regrowth of native grasses in general (Bates et al., 2007; Rose and Eddleman, 1994), and may also stimulate invasion (Owen et al., 2009). We found that shredding increased the frequency of only three of the four dominant grasses that we studied. The number of years since the disturbance
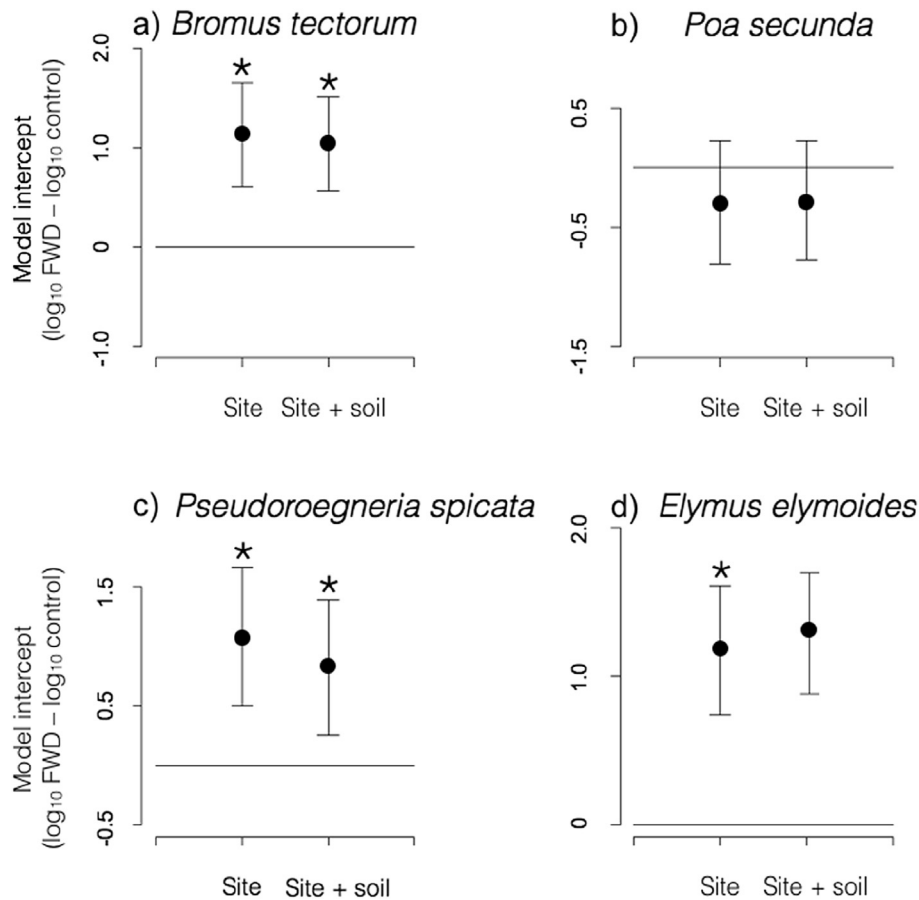
Fig. 3. The exotic annual, *Bromus tectorum*, and two native perennial grasses *Elymus elymoides* and *Pseudoroegneria spicata* increased in frequency following FWD, and soil characteristics explained the variation in species responses. For each of the four species, the intercepts, μ_α, from two different mixed models are presented, one that included woodland sites as a random effect and time since FWD addition as a covariate (site), and another that included location and time but also soil variables (site + soil, $n = 31$). If soil variables explained any of the variation in grass frequencies, then the model intercept including soil variables should be closer to zero than the intercept excluding soil variables. Significant intercepts (i.e., 95% confidence interval of the intercept did not include zero) and reductions in the model intercept including soils are indicated with an asterisk.

occurred intensified the effects of shredding on the native grasses but diminished the effects on the exotic. In general, links between soils and grass species occurred predominantly in deeper soils (i.e., soil respiration, net N mineralization, and microbial biomass). However, FWD-induced shifts in soils explained up to 41% of species responses of only two species, *B. tectorum* and *P. spicata*. Unexpectedly, fertile areas associated with tree-islands did not structure the frequency of any grass species. Our results demonstrate the importance of plant-soil-microbial interactions in mediating the ecological effects of a disturbance, and highlight that these interactions may occur deeper in the soil profile away from the initial disturbance.

4.1. Grass-specific response to FWD and soils

Contrary to our hypothesis, we found that the effects of FWD on soils did not necessarily influence the frequencies of all four grasses but may simultaneously facilitate exotic invasion and promote native grass establishment. For example, for exotic *B. tectorum* and native *P. spicata*, the contribution of our measured soil nutrient and microbial activity variables explained 25% and 41% of their frequency, respectively. However, *E. elymoides* frequency was not directly related to any of our measured soil variables, and *P. secunda*, although insensitive to woody addition, was influenced by P availability. The remaining variation in *B. tectorum*, *P. spicata*, and *P. secunda* and all the variation in *E. elymoides* frequencies were

most likely controlled by other variables, such as external climate drivers like intra- and inter-annual precipitation variability and ecohydrological shifts caused by FWD and tree removal. Rainfall inputs and soil moisture dynamics often drive grass seedling survival in arid and semi-arid ecosystems (Abbott and Roundy, 2003), with relatively small changes in the timing or the amount of rainfall translating into consequence for plant population dynamics and species coexistence (Peters et al., 2014). Also, FWD and tree removal increases water availability for remaining plant species by decreasing rainfall interception and the amount of water lost due to evapotranspiration fluxes (Roundy et al., 2014a). For example, *J. osteosperma* removal increased the number of wet or relatively moist days (> -1.5 MPa) by at least a month to a soil depth of 30 cm (Young et al., 2013).

4.2. Deep instead of shallow soils influenced grasses

Unexpectedly, our results suggest that the effects of FWD on biology may extend deep into the soil profile, potentially deeper than the effects of woody materials on soil chemistry that extend only a few centimeters (Spears and Lajtha, 2004). We hypothesized that surface and not subsurface soils would dominant FWD-induced links between soil processes and species. Surface soils contain germinating grasses that are in direct contact with shredded materials. Thus, if soils mediated grass responses to FWD, we believed we would see these effects chiefly in surface soils. But
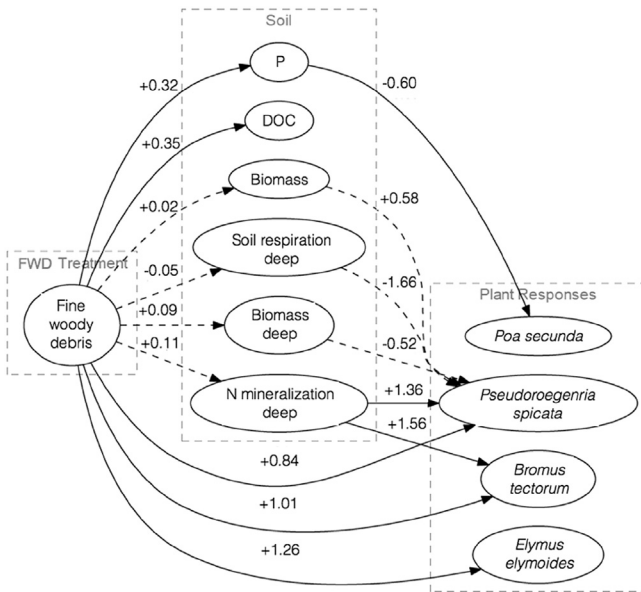
Fig. 4. Changes in soils due to FWD partially mediated the effects of FWD addition on the exotic *B. tectorum* and native *P. spicata* and *Poa secunda*. The mixed model identifies links between soil variables and species frequency that were influenced by FWD ($n = 31$). Values are estimated unstandardized parameters. The model includes woodland locations as a random effect, and time since treatment or shredding as a covariate. The links between parameters (arrows) and corresponding values can be roughly interpreted as the percent change in the response variable (the one at the head of the arrow) given a 1% change in the explanatory variable (the one at the tail of the arrow). Solid arrows between soil variables and grass frequencies indicate effects that were significant ($p < 0.05$) and dashed arrows indicate marginally significant effects ($0.05 < p < 0.07$) between variables and grasses.

two-thirds of the microbial-mediated processes influencing grasses occurred in deeper soils. The importance of deeper soil may have stemmed from FWD constituents leaching through the soil profile, but the decomposition of shredded piñon and juniper root systems most likely aided in altering processes. Root systems in these woodlands constitute 25–40% of the total tree biomass (Miller et al., 1990) and are composed of mostly fine roots at our deep sampling depth (12–17 cm; Peek et al., 2006). Fine roots are relatively more labile than woody C substrates. Thus, over the last 1–8 years since shredding, the decaying root system, and not FWD, may have influenced our significant, deep soil processes (i.e., net N mineralization, respiration, and microbial biomass) to a greater extent. Unfortunately, we did not experimentally separate FWD from root effects on nutrient availability. Additionally, the reason for the limited links in surface soils may stem from the effects of FWD being masked by the relatively thick layer of litter and duff (partly decomposed organic matter or unrecognizable plant forms) existing between the woody additions and the soil mineral surface. *Juniper osteosperma* trees generate immense amounts of litter and duff beneath their canopies and these materials may continue to influence soil microorganisms more than FWD even following the disturbance.

4.3. Time since disturbance and not microsite structured grass responses

Surprisingly, tree-island microsites failed to improve the fit of any our models. We hypothesized and expected fertile areas (i.e., canopy and edge microsites) to increase grass species frequency following FWD additions. Shredded materials in manipulative studies have increased grass seedling emergence, establishment, and survival by adding more nutrients to already relatively fertile

tree-island soils and trapping moisture in the spring (Young et al., 2013). Due to our post-hoc design, we may have missed the importance of microsites in structuring plant responses. We measured all existing grass species and not just the new individuals emerging since shredding. The number of years since shredding consistently reduced the uncertainty surrounding the FWD-induced soil effects on grass frequencies, but the way that time influenced grasses differed between the annual and perennials. The negative time intercept for *B. tectorum* suggested that the effects of shredding were diminishing with time, while a positive time intercept for *P. spicata* and *P. secunda* suggested that the effects of FWD were intensifying. Our results support other findings where an increase of native plants, especially perennial plants, started to occur a couple of years after treatment and continued to increase in frequency with each additional year (Rose and Eddleman, 1994; Bates et al., 2007). FWD requires decades to decompose, but possibly the changes in the annual *B. tectorum* are realized relatively quickly (i.e., the first few years) due the species being an opportunistic competitor and a prolific seed producer. Alternatively, the impact of FWD on perennial grasses may require multiple years to become apparent as certain native species benefit or contend with FWD-induced changes in soils to survive and produce seed.

4.4. Deep soil N but not P stimulated exotic and native grasses

Consistent with our hypothesis, net N mineralization, instead of soil respiration or microbial biomass, dictated the highest number of grass species responses following FWD. In deep soils, higher N availability stimulated the frequencies of both the exotic *B. tectorum* and *P. spicata*. In N-limited ecosystems, like piñon-juniper woodlands, inorganic N pools, especially in surface soils, are highlighted as an integral factor influencing grass species success (James et al., 2008). For example, during invasion, *B. tectorum* reduced soil inorganic N pools in the top 5 cm of soil by as much as 50%, indicating the potential importance of N to the success of this exotic (Rimer and Evans, 2006). However, both of these species are known to utilize deeper soil N resources with the native perennial actually acquiring similar levels of inorganic N from shallow and deep N pools (James et al., 2008). Our results suggest that these deeper soil resources altered by FWD enhanced the survival and/or growth of the exotic and native alike by possibly providing inorganic N to new establishing grasses and offering more N to already established perennial roots. As stated previously, the new N was most likely derived from organic matter being translocated within the profile and/or the decaying root system of the shredded tree.

Unexpectedly, higher levels of P availability associated with FWD elicited no response among grasses and actually depressed the frequency of native *P. secunda*. Generally, soil P availability is low in arid and semi-arid environments and potentially limits the growth of grasses (Caldwell et al., 1987). Three of our four grasses were relatively insensitive to changes in P availability. We find it difficult to explain why higher levels of a limiting nutrient depressed plant frequency, but it may stem from differences in grass species adaptations to low nutrient environments. Piñon-juniper woodlands and grass species often establish on calcareous soils that strongly dictate the adsorption and precipitation of P (Caldwell et al., 1991). In these soils, P is most often bound by carbonates and free calcium, and grass species differ in their ability to mobilize P via root exudates (e.g., phosphatase and inorganic acids; Marschner et al., 2006). If *P. secunda* was adapted to effectively sequester relatively immobile P and the addition of FWD increased the availability of P, then this native may have lost its competitive advantage over other grass species and decreased in frequency. Alternatively, to help sequester P many grasses,

including *Poa* species, are facultatively mycorrhizal (Vandenkoornhuyse et al., 2003) and mycorrhizal colonization in grasses tends to decline following P fertilization (Eom et al., 1999). Thus, following higher P concentrations induced by FWD, *P. secunda* may have lost the competitive benefits associated with its mycorrhizal mutualism and decreased in frequency.

4.5. Microbial activity and native P. spicata

The depression of deep respiration following our FWD additions was associated with a reduction in native *P. spicata* frequency. The addition of woody debris necessarily coincides with changes in microbial metabolism. In the short-term (i.e., days to year), metabolism is enhanced by a flush of labile C substrates (e.g., leaves, bark, and twigs) entering soils, while in the long-term (i.e., years to decade), soil respiration may be depressed by the more recalcitrant C sources, such as lignin (Dehlin et al., 2006). The direct effect of soil respiration on plants is unclear. However, the lower respiration rates under FWD additions may signal a decline in other processes associated with microorganisms. For example, a decline in microbial activity may be related to a depression in the release rates of essential plant micronutrients (Ranjbar and Jalali, 2012), or a reduction in soil water holding capacity and retention due to less extracellular polymeric substances being produced from metabolizing bacteria (Or et al., 2007). Thus, other abiotic and biotic processes, indirectly associated with lower levels of respiration, may have negatively influenced *P. spicata*.

As for microbial biomass, increases in biomass caused divergent effects on *P. spicata* by depth. In surface soils, microbial biomass, such as growth promoting rhizobacteria, possibly aided the establishment of seedlings. Bacterial species, such as Actinobacteria, known to promoted seedling emergence and growth (Hayat et al., 2010), are common in the rhizospheric soils of semi-arid grasses (Chen et al., 2015). Alternatively, in deeper soils, microbial biomass reduced *P. spicata* frequency. Changes in biomass are often accompanied by shifts in microbial community composition, which may influence grasses (Eom et al., 1999; Vandenkoornhuyse et al., 2003). For example, if FWD altered the mycorrhizal species diversity and richness in soils and the beneficial relationship between fungi and *P. spicata*, then *P. spicata* may be negatively impacted by FWD.

4.6. FWD and grass species advice to land managers

As land mangers attempt to stem wildfires, the practice of shredding whole trees and the FWD it produces stimulates the establishment and persistence of exotic and native grass species alike. Thus, shredding may reduce the biomass of standing fuels (i.e., standing trees) but as grasses establish, the resulting biomass may act as a bridge to help fires jump breaks. The effects of FWD on grasses continued to intensify with time for perennials, but not for the exotic grass, suggesting that to gauge the effects of shredding on invasion or native grass establishment ecosystems should be monitored multiple times through time. Soils were important in understanding the effects of FWD on grass frequencies, especially in deep soils away from the layer of FWD on the surface. Deep soil processes are often overlooked in linking belowground and aboveground responses, but to be able to predict the changes in grass species after shredding, land mangers should measure nutrient availability through the soil profile. Deep increases in net N mineralization, but not P availability, facilitated the increase of *B. tectorum* and *P. spicata* after shredding, suggesting that N and not P limit grass frequencies. Additionally, soil respiration and microbial biomass also influenced grass frequencies. But to more fully explain these relationships, future studies need to link other microbial-mediated processes (e.g., micronutrients, soil water relations) and specific bacterial and fungal species (e.g., growth promoting bacteria and mycorrhizae) to grass response. Ultimately, microbial activity and nutrients only partially explained the frequency of three of the four grasses that we studied demonstrating that multiple other variables, like physiochemical soil properties and external climate drivers, have the potential to also mediate the impact of FWD on grasses.

Author contributions

ZTA, DR, JB, and BR designed the study. ZTA, DR, JB, and TC conducted the experiments. ZTA, DR, TC, and BR analyzed and interpreted the data, and all authors helped write and review the manuscript. ZTA agrees to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2016.11.002.

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