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SPECIAL FEATURE: ORIGINAL ARTICLE

Linking Genome to Ecosystem

Forest gene diversity is correlated with the composition and function of soil microbial communities

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Abstract The growing field of community and ecosystem genetics indicates that plant genotype and genotypic variation are important for structuring communities and ecosystem processes. Little is known, however, regarding the effects of stand gene diversity on soil communities and processes under field conditions. Utilizing natural genetic variation occurring in *Populus* spp. hybrid zones, we tested the hypothesis that stand gene diversity structures soil microbial communities and influences soil nutrient pools. We found significant unimodal patterns relating gene diversity to soil microbial community composition, microbial exoenzyme activity of a carbon-acquiring enzyme, and availability of soil nitrogen. Multivariate analyses indicate that this pattern is due to the correlation between gene diversity, plant secondary chemistry, and the composition of the microbial community that impacts the availability of soil nitrogen. Together, these data from a natural system indicate that stand gene diversity may affect soil microbial communities and soil processes in ways similar to species diversity (i.e., unimodal patterns). Our results further demonstrate that the effects of plant genetic diversity on other organisms may be mediated by plant functional trait variation.

Keywords Community and ecosystem genetics · Extracellular enzyme activity · Functional traits · Genetic diversity · *Populus* · Unimodal diversity patterns

Introduction

Understanding the mechanisms by which phenotypic variation in one species affects interactions with others and

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regulates energy flow and biogeochemical cycles is fundamental for linking genes to ecosystems. Making such links is important because ecosystems provide services, such as food and fiber production, and therefore worldwide changes to species and genetic variation may have extended consequences (Whitham et al. 2003, 2006). Recent studies have shown that genetic variation in plants (measured in multiple ways; Hughes et al. 2008) can have interspecific community consequences affecting associated plant (Iason et al. 2005), arthropod (Bailey et al. 2006; Crutsinger et al. 2006; Barbour et al. 2009a, b; Johnson et al. 2009), and soil microbial communities and their activities (Madritch et al. 2006, 2009; Schweitzer et al. 2008a) in a variety of plant species. Moreover, genetically based variation in these species interactions can result in variation to ecosystem processes such as productivity, energy flow, and nutrient cycles (Treseder and Vitousek 2001; Schweitzer et al. 2004; Bailey et al. 2006; Madritch et al. 2006, 2009).

While studies focused on the genetically based links between plants and soils are still rare, studies at the species and functional group level in both agricultural and natural systems commonly demonstrate effects on soil microbial community composition or activity and subsequent soil processes (Hobbie 1992; Bever et al. 1996; Hooper et al. 2000; Diab el Arab et al. 2001; Bartelt-Ryser et al. 2005); for example, many studies have documented that soil microbial communities, leaf litter decomposition, and mineralization processes differ in soils beneath different dominant tree species that possess different plant traits (Pastor et al. 1984; Zak et al. 1986). These differences are likely due to differences in plant growth rate, leaf and root chemistry or production, root exudation or abiotic effects due to different canopy structure. Plant trait variation consequently influences substrate availability or conditions for soil microorganisms that may influence microbial community composition and activity (Bever et al. 1996; Paul and Clark 1996; Priha et al. 2001; Bartelt-Ryser et al. 2005; Grayston and Prescott 2005). Such variation in species (and their traits) has led to somewhat predictable patterns of ecosystem processes when examined in species diversity studies. Experimental studies commonly find a unimodal pattern when examining the effects of species diversity on patterns of productivity or soil processes (Waldrop et al. 2006). This unimodal pattern is thought to be a result of shifts in resource use and acquisition with increasing species diversity (Mittelbach et al. 2001; Bond and Chase 2002; Chase and Leibold 2002). Links between plant traits and belowground processes in terrestrial ecosystems (Hobbie 1992; Hooper et al. 2000; Wardle et al. 2004) suggest that genetic variation in dominant plant species could influence the associated belowground soil microbial community, and the ecosystem processes that microorganisms mediate, based on the same mechanisms that structure plant–soil interactions at the species level (Zinke 1962; Rhoades 1997; Smith et al. 1999).

Genetic individuals (i.e., genotypes) within a species vary in a multitude of traits including, but not limited to, growth rates, secondary chemistry, physiological processes (i.e., photosynthesis and water use/loss), and ontogeny that have been shown to impact other species (Bossdorf et al. 2009; Hughes et al. 2009; Clark 2010). Variation in plant traits can directly or indirectly influence associated species, such as herbivores and their predators on plants (Bailey et al. 2006; Shuster et al. 2006; Simchuk 2008) and fungi and bacteria associated with a plant genotype or the soils beneath them (Kasurinen et al. 2005; Schweitzer et al. 2008a; Holeski et al. 2009; Karst et al. 2009), thereby creating unique communities on individual plants. These community interactions can extend to affect ecosystem processes associated with individual genotypes (Schweitzer et al. 2005; Madritch et al. 2006, 2009; M.D. Madritch and R.L. Lindroth, unpublished data); for example, *Populus* genotypes vary in suites of phenotypic traits, such as productivity (Lojewski et al. 2009) and secondary chemistry (Rehill et al. 2006; Bailey et al. 2006), that can condition their associated soils, via litter inputs, to structure microbial community composition, pools of microbial nitrogen (N; Schweitzer et al. 2008a; Madritch et al. 2009), and rates of net N mineralization (Schweitzer et al. in press).

Despite the growing evidence that individual plant genotypes can structure associated soil communities and the processes in soil that microorganisms mediate, few data exist from natural systems to understand the effects of stand genetic variation on soil communities and the biogeochemical processes they mediate. We addressed the potential role of plant genetic variation in plant–soil linkages utilizing a model system and stands of trees with known gene diversity (i.e., variation in heterozygosity based on molecular markers; Wimp et al. 2004). Utilizing this natural system, we addressed hypotheses relating the relative importance of average stand gene diversity to soil microbial communities and soil nutrient pools. Based on previous work finding a positive relationship between stand gene diversity (i.e., heterozygosity) and arthropod community diversity (Wimp et al. 2004), we hypothesized that average stand gene diversity would influence soil microbial community composition, exoenzyme activity, and soil nutrient pools. Additionally, we examined whether soil communities and processes would be related linearly to plant gene diversity as in Wimp et al. (2004) or would instead follow a unimodal (or quadratic fit) relationship and be related to functional plant traits. Together, these hypotheses address the ecosystem consequences of plant genetic diversity on associated soil communities and the processes they mediate in natural field conditions.

Methods

We studied 11 natural riparian *Populus* spp. stands along a 13-km reach of the Weber River, near Ogden, Utah, to assess the influence of the genetic composition of the dominant trees on soil communities and processes. Each stand contained a different natural composition of *Populus* spp. (*Populus fremontii*, *P. angustifolia*, and their natural F_1 and backcross hybrids). Each stand was 1.8–2.6 ha^2 in area and was separated by natural or manmade boundaries with estimated per-stand density of *Populus* sp. of 664.04 stems $ha^{-1} \pm 55.7$ standard error (SE), and basal area of 29.03 m^2 $ha^{-1} \pm 4.07$ SE [based on a measurement of 43, 116.7-m^2 circular plots (2–8 per stand)]. All sites were located at 1300 m in elevation. Regional weather station data indicated that all sites experienced similar climates (mean annual temperature ~10.7°C, mean annual precipitation ~410 mm; data from the Ogden Pioneer Park weather station). All sites had sandy-skeletal, mixed, mesic, Entic Haploxeroll soils with pH that varied between 7.2 and 7.6. In each stand, 20 randomly chosen trees were subjected to amplified fragment length polymorphism (AFLP) analysis to assess plant gene diversity. Plant gene diversity (Weir 1996) for each stand was quantified using average heterozygosity. We used the frequency of the null allele and assumptions of Hardy–Weinberg equilibrium to determine expected heterozygosity at a particular locus, and values were averaged across all loci (see Wimp et al. 2004 for more details on these analyses). Additionally, because previous work with *Populus* spp. indicated the importance of foliar secondary compounds to soil processes (Schweitzer et al. 2004, 2008b; Madritch et al. 2006, 2007), we quantified the concentration of condensed tannins (CTs) during the height of the growing season from individual trees from all 11 stands. Leaf tissue from five individual trees (5 of the 20 in which AFLP analyses were conducted) was collected on dry ice in the field and then freeze-dried in the laboratory. Condensed tannins were extracted from finely ground leaf tissue with sequential application of 70% acetone + 10 mM ascorbic acid. Condensed tannins were quantified using the butanol–HCl method from Porter et al. (1986) and recorded as percent leaf tissue dry weight. Standards used in the analysis were CTs purified from *P. angustifolia* using the method of Hagerman and Butler (1989).

Soil was collected to assess a suite of microbial community traits including microbial community composition, with phospholipid fatty acid (PLFA) biomarkers, potential activity of the microbial community with exoenzymes (extracellular enzymes), and pools of microbial and soil carbon (C) and nitrogen (N). Soil N availability was assessed with ion-exchange resin techniques. In both July and November, soils were collected (with a 6.25 × 15 cm diameter soil hammer) from 10 random locations (i.e., both beneath trees or in interspaces, wherever the random location was identified) within each stand and pooled ($n = 11$). At each collection date, mineral soils were collected between 0 and 15 cm depth, kept cool on ice until they were brought to the laboratory, and stored at 4°C until analysis. Soils were sieved (<2 mm) to remove coarse fragments and roots, and a subsample was immediately freeze-dried. From these freeze-dried samples, we assessed microbial community composition with PLFA biomarkers using the method of White and Ringleberg (1998). The freeze-dried soil was extracted with a phosphate-buffered chloroform–methanol solvent (Bligh and Dwyer 1959) and separated into functional classes of signature fatty acids after methylation of the polar lipids and analysis by gas chromatography [White et al. 1979; GC-mass spectrometer (6890N GC/5973N MSD); Agilent Technologies, Palo Alto, CA, USA]. The PLFAs are indicative of major microbial groups (e.g., Gram-positive and Gram-negative bacteria, actinobacter, and fungi; White et al. 1979; Zelles 1999; Leckie 2005). We conservatively used common PLFAs between 14 and 18 C atoms long to include in the analysis, as these are PLFAs identified as exclusively microbial. PLFA compounds identified as general bacterial (14:0, i15:0, a15:0, 15:0, i16:0, 10me16, 16:1ω9, 17:0, cy17:0, 18:0) and fungal biomarkers (18:1ω9c, 18:2ω6t, 18:2ω6c) were used to calculate the ratio of bacterial to fungal PLFA concentration in the soils (O'Leary and Wilkinson 1988; Wilkinson 1988; Frostegård et al. 1993; Frostegård and Bååth 1996; Zelles 1999).

We quantified microbial C (November date only) and N (July and November dates) pools using the chloroform fumigation extraction method (Brookes et al. 1985; Vance et al. 1987). A subsample of field-moist soil (~25 g) was extracted with 50 ml 0.5 M K_2SO_4, shaken, gravity-filtered with Whatman filter paper no. 1 (leached with deionized water and 0.5 M K_2SO_4), and stored in a freezer until chemical analysis. Another 25-g field-moist subsample was exposed to chloroform for 5 days in a glass vacuum desiccator with 30 ml ethanol-free chloroform. After the fumigation period, samples were extracted with 50 ml 0.5 M K_2SO_4 in the same manner as above. Total microbial N was determined on the thawed extracts with a micro-Kjeldahl digestion followed by colorimetric analysis using the salicylate method on a Lachat AE auto-analyzer (Lachat Industries, Inc., Loveland, CO, USA). Microbial N was determined by subtracting the total N in the unfumigated sample from the total N in the fumigated sample. Total C in fumigated and unfumigated subsamples was determined by ultraviolet-enhanced persulfate oxidation using a Dohrmann DC-80 carbon analyzer (Tekmar–Dohrmann, Cincinnati, OH, USA). Similarly to microbial N, microbial C was determined by subtracting the total

organic C in the unfumigated sample from the total organic C in the fumigated sample. For both microbial N and C values, no extraction efficiency factors (i.e., k_{EN} or k_{EC}) were used to adjust these fumigation flush values.

We quantified soil total C and total N pools on air-dried soil from the November collection date. The samples were ground with a pestle and mortar to a fine powder and run on a Thermo-Finnigan Delta^{plus} Advantage gas isotope-ratio mass spectrometer interfaced with a Costech Analytical ECS4010 elemental analyzer (Thermo Fisher Scientific, Inc., Waltham, MA, USA). A subsample of field-moist soil was oven-dried (48 h at 105°C) to determine soil moisture content. All PLFA, enzyme activity, microbial biomass, and total C and N values are expressed on an oven-dry mass basis.

We quantified potential soil microbial exoenzyme (i.e., extracellular enzyme) activities (November date only) that are involved in C, N or phosphorus (P) cycling (sensu Saiya-Cork et al. 2002; Tabatabai and Dick 2002; Waldrop et al. 2004; Sinsabaugh 2010). Immediately after sieving, the activities of eight enzymes were assessed for all soil samples (1.0 g soil in 50 mmol/L sodium acetate buffer, pH 6): α-1,4-glucosidase (EC 3.2.1.20), β-1,4-glucosidase (EC 3.2.1.21), sulfatase (EC 3.1.5), β-1,4-xylosidase (EC 3.2.1.37), β-1,4-*N*-acetylglucosaminidase (EC 3.1.6.1), phenol oxidase (EC 1.10.3.2), peroxidase (EC 1.11.1.7), and phosphatase (EC3.1.3.2). We analyzed eight analytical replicates per sample for each enzyme. The incubation times for each enzyme were as follows: phosphatase and *N*-acetylglucosaminidase 0.5 h; β-glucosidase, α-glucosidase, β-xylosidase, and sulfatase 2 h; phenol oxidase and peroxidase 24 h. The substrate methyl-umbelliferone (MUB) was used for fluorometric analysis of α-glucosidase, β-glucosidase, β-xylosidase, sulfatase, *N*-acetylglucosaminidase, and phosphatase (SpectraMax Gemini EM fluorimeter; Molecular Devices Corp., Sunnyvale, CA, USA). Colorimetric analysis with the substrate L-3, 4-dihydroxy-phenylalanine (L-DOPA) was used to quantify phenol oxidase and peroxidase in duplicate plates with and without addition of 0.3% H_2O_2 (SpectraMax Plus384 spectrophotometer; Molecular Devices Corp., Sunnyvale, CA, USA). Phenol oxidase activity was indicated by L-DOPA metabolism without H_2O_2, and peroxidase activity was measured as the difference between L-DOPA metabolism with and without H_2O_2 (Sinsabaugh 2010).

We used the ion-exchange resin (IER) bag method (Hart and Firestone 1989) to assess the availability of inorganic N across the treatments. We buried 24 IER bags in random locations at each stand. Approximately 25 g mixed-bed, IER (J.T. Baker, Phillipsburg, NJ, USA; Hart et al. 1994) was placed into nylon bags and buried at depth of 15 cm, installed at an angle to minimize soil disturbance on top of each bag. The resin bags were incubated in situ for 6.5 months during the growing season (1 May–15 November). After incubation, the resin bags were collected into individual paper sacks, air-dried, and then extracted with 100 ml 2 M KCl. The filtered extracts (filtered after first rinsing with deionized water and then 2 M KCl) were then frozen until analysis of ammonium and nitrate on a Lachat AE flow-injection auto-analyzer (Hart et al. 1994; Lachat Industries, Inc., Loveland, CO, USA), as in Fischer et al. (2010). A subsample of air-dried, unincubated resin was oven-dried (70°C for 48 h) to allow final data to be expressed on an oven-dry mass basis.

Statistical analyses

To address the hypothesis that stand gene diversity was related to the soil microbial community, exoenzyme activities or soil nutrient pools, we used a generalized linear model (GLM) in which gene diversity was characterized as a fixed effect. We compared the soil response variables to stand gene diversity as a linear function (sensu Wimp et al. (2004), in which stand gene diversity was linearly related to arthropod community diversity), as well as a quadratic function, as previous work with species diversity effects indicated that intermediate levels of species diversity have the highest overall plant productivity or process rates at local scales (sensu Bond and Chase 2002). Where relationships between stand gene diversity and soil dynamics were found to be significant, we expanded our model to include known mechanistic links, such as stand average CT concentration and soil microbial community composition, as characterized by the scores from the non-metric multidimensional scaling (NMDS) ordination (see Shuster et al. 2006 for a similar use of this procedure). The use of the *x*-axis from the NMDS ordination allows us to compare the Bray–Curtis distance, which indicates variation in community composition, with other response variables. All GLM multiple regressions were run using JMP 8.0 (SAS Institute, Cary, NC, USA).

Results

We found significant unimodal relationships between stand gene diversity and soil microbial community composition (measured on the November date only), soil bacteria-to-fungi ratio (measured on the November date only), β-1,4-glucosidase activity, and soil N availability (Table 1); however, we found no relationship between stand gene diversity and microbial or total soil N, C or the other 7 exoenzymes we assayed (although 4 additional exoenzymes were marginally significant with *P* values between 0.05 and 0.10). We found correlations between several aspects of the soil microbial community (as quantified from the ordination

Table 1 Stand tree gene diversity has variable effects on soil microbial communities, microbial activities, and nutrient pools ($n = 11$). Generalized linear model regression was performed to test the hypotheses that there were linear or quadratic relationships of stand gene diversity across natural stands of *Populus* spp. and microbial pools of nitrogen (N; mg N/kg) and carbon (C; mg C/kg), phospholipid fatty acid biomarkers (PLFA; μmol/g), potential extracellular enzyme activity (μmol g^{-1} h^{-1}), pools of total soil N (mg N/kg) and C (mg C/kg) as well as N availability (μg N g^{-1} day^{-1}). Chi-square values and *P* values are shown; significant *P* values ($\alpha = 0.05$) are shown with an asterisk and in bold

Response variable	Gene diversity-linear		Gene diversity-quadratic	
	χ^2	*P* value	χ^2	*P* value
Community composition				
PLFA composition† (July)	0.451	0.50	2.574	0.11
PLFA composition†(November)	1.095	0.30	**5.718**	**0.02***
PLFA bacteria-to-fungi ratio (July)	1.130	0.29	0.887	0.35
PLFA bacteria-to-fungi ratio (November)	0.784	0.38	**3.856**	**0.05***
Nutrient pools				
Microbial N (July)	0.041	0.84	1.007	0.32
Microbial N (November)	0.717	0.40	0.858	0.35
Microbial C (November)	0.003	0.95	3.437	0.06
Total soil N (November)	0.600	0.44	0.528	0.47
Total organic soil C (November)	0.136	0.73	0.066	0.80
Soil C-to-N mass ratio (November)	1.691	0.19	2.992	0.08
NH_4^+	1.172	0.28	**10.876**	**0.001***
NO_3^-	0.034	0.89	**6.813**	**0.009***
Total inorganic N	0.119	0.73	**6.103**	**0.01***
Microbial activity				
α-1,4-Glucosidase activity	0.653	0.42	0.798	0.37
β-1,4-Glucosidase activity	0.680	0.74	**4.358**	**0.04***
Sulfatase activity	3.095	0.08	3.638	0.06
β-1,4-Xylosidase activity	0.025	0.88	2.727	0.10
β-1,4-*N*-acetylglucosaminidase activity	1.638	0.20	0.478	0.49
Acid phosphatase activity	0.539	0.46	3.209	0.07
Phenol oxidase activity	0.004	0.95	0.018	0.90
Peroxidase activity	**4.035**	**0.05***	2.656	0.10

† *x*-axis from a nonmetric multidimensional scaling (NMDS) ordination (sensu Shuster et al. 2006)

score of PLFA biomarkers, the ratio of soil bacteria to fungi, and microbial activity of β-1,4-glucosidase, a carbon-degrading exoenzyme) and stand gene diversity (Fig. 1); as the community ordination is based on Bray–Curtis distances, we cannot apply direction to that change. Moreover, we found soil NH_4^+, NO_3^-, and total inorganic N ($NH_4^+ + NO_3^-$) availabilities, as assessed by IER bags, were highest at intermediate levels of gene diversity (Fig. 2), similar to the patterns with the carbon-degrading exoenzyme; the ratio of bacteria to fungi also showed unimodal relationships but was lowest at intermediate levels of gene diversity (i.e., fungi dominated). We do not know if the difference in N availability is due to differential N turnover in stands with varying litter inputs or due to variation in tree N uptake rates in the stands composed of varying tree compositions; however, either mechanism suggests that tree composition affects soil N availability (Binkley and Hart 1989).

Because the concentration of foliar CTs can have important inhibitory effects on microbial communities and their activities (Hättenschwiler and Vitousek 2000; Kraus et al. 2003) and *Populus* spp. exhibit high genetic variation for this trait (Schweitzer et al. 2008b), we included foliar CTs in the regression model. Additionally, to test the hypothesis that the composition of the microbial community itself may be important for soil N availability (sensu Waldrop et al. 2000; Dang et al. 2005; Strickland et al. 2009), we included soil microbial community composition (using the ordination scores from the PLFA similarity matrix) along with gene diversity and foliar CT in the model. Including these factors in the model allowed us to test the combined importance of foliar CTs ($\chi^2 = 8.676$, $P = 0.003$), microbial community composition ($\chi^2 = 7.006$, $P = 0.008$), and stand gene diversity (linear fit: $\chi^2 = 6.172$, $P = 0.013$; quadratic fit: $\chi^2 = 14.367$,

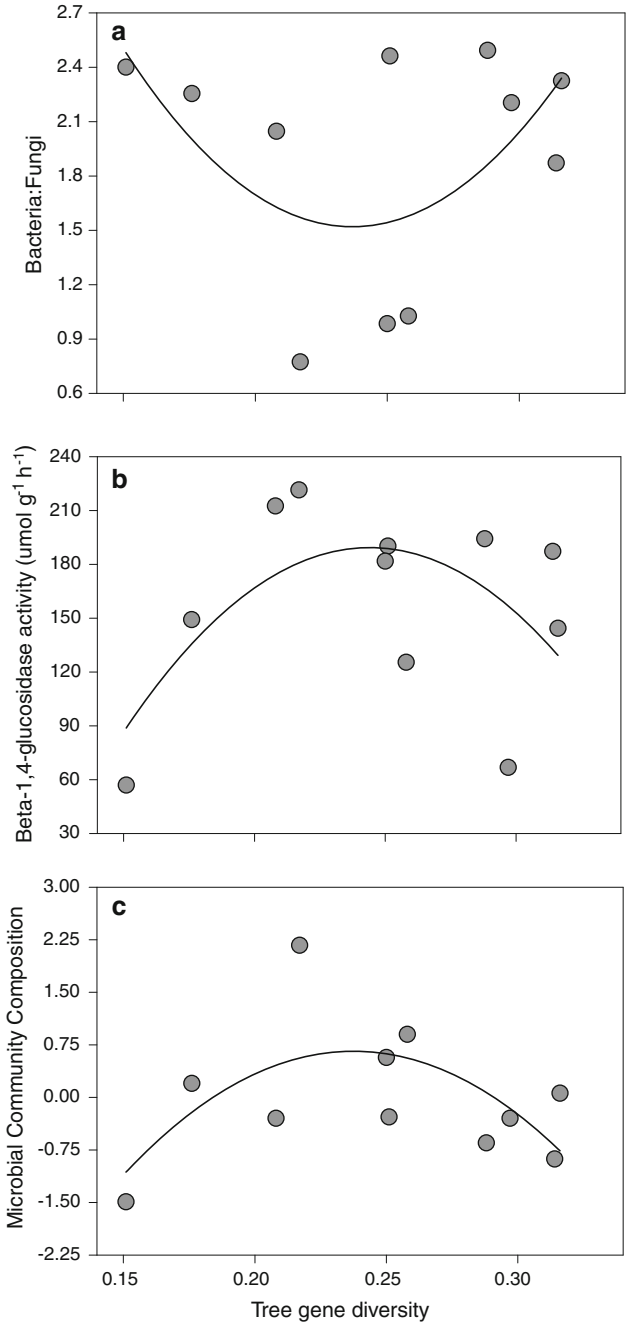

Fig. 1 Stand gene diversity (i.e., heterozygosity) is nonlinearly correlated to soil microbial community composition or microbial activities. The ratio of bacteria to fungi based on phospholipid fatty acid (PLFA) biomarkers (**a**) is negatively related to tree gene diversity, while the activity of a carbon-degrading exoenzyme β-1, 4-glucosidase (**b**) is positively related to tree gene diversity. The composition of the microbial community (**c**; as determined by ordination scores from the PLFA biomarker distance matrix) changes as gene diversity changes

$P = 0.002$) to the availability of NH_4^+ in the soil. For soil NO_3^- availability, CTs ($\chi^2 = 0.904$, $P = 0.342$) and the composition of the microbial community ($\chi^2 = 1.52$, $P = 0.22$) were less important than stand gene diversity (linear fit: $\chi^2 = 0.056$, $P = 0.81$; quadratic fit: $\chi^2 = 5.723$, $P = 0.017$). Similarly, for total inorganic N ($NH_4^+ + NO_3^-$) availability in the soil, stand gene diversity (linear fit: $\chi^2 = 0.912$, $P = 0.34$; quadratic fit: $\chi^2 = 6.169$, $P = 0.013$) was more important than foliar CTs ($\chi^2 = 1.539$, $P = 0.215$) or the composition of the microbial community ($\chi^2 = 2.73$, $P = 0.10$). The model for soil bacteria-to-fungi ratio indicated that gene diversity (linear fit: $\chi^2 = 0.773$, $P = 0.38$; quadratic fit: $\chi^2 = 4.037$, $P = 0.04$), but not CTs ($\chi^2 = 0.427$, $P = 0.51$), was important for determining soil bacterial and fungal abundance; microbial community composition was not included in this model as the bacteria-to-fungi PLFA values are a subset of the total microbial community composition. These results overall indicate that stand gene diversity, foliar CTs, and the composition of the microbial community are all significant factors affecting availability of NH_4^+ in soil. In contrast, unknown plant phenotypic traits, associated with stand gene diversity (or other unknown factors), are related to the soil bacteria-to-fungi ratio, availability of NO_3^-, and total inorganic N in the soil.

Discussion

Overall, we found two main patterns that supported our initial hypotheses of a correlation between stand gene diversity and soil microbial community composition, microbial activity, and soil nutrient pools. We found that: (1) soil microbial community composition (as quantified by ordination scores of PLFA biomarkers) changed as gene diversity changed, and that the activity of β-1,4-glucosidase and the availabilities of soil NH_4^+, NO_3^-, and total inorganic N were highest at intermediate levels of gene diversity (the ratio of bacteria to fungi was lowest at intermediate levels); and (2) mechanistically, stand gene diversity, foliar CTs, and the composition of the microbial community all covaried with the availability of NH_4^+ in the soil. In contrast, unknown phenotypic factors related to gene diversity were correlated to the ratio of soil bacteria to fungi and the availabilities of NO_3^- and total inorganic N in the soil. While this is an observational study and other unmeasured causative factors cannot be eliminated, these data are some of the first of their kind to be collected in the field (i.e., outside of controlled common garden environments; see also Madritch et al. 2009) to confirm previous common garden studies of the importance of genetic-based linkages between plants and soils. Moreover, the linkage of plant traits to some of these soil processes suggests that the patterns we observed were likely due to the variation in plants and not vice versa. These data, overall, suggest that, first, stand gene diversity may be analogous to species diversity in that unimodal patterns are found with soil

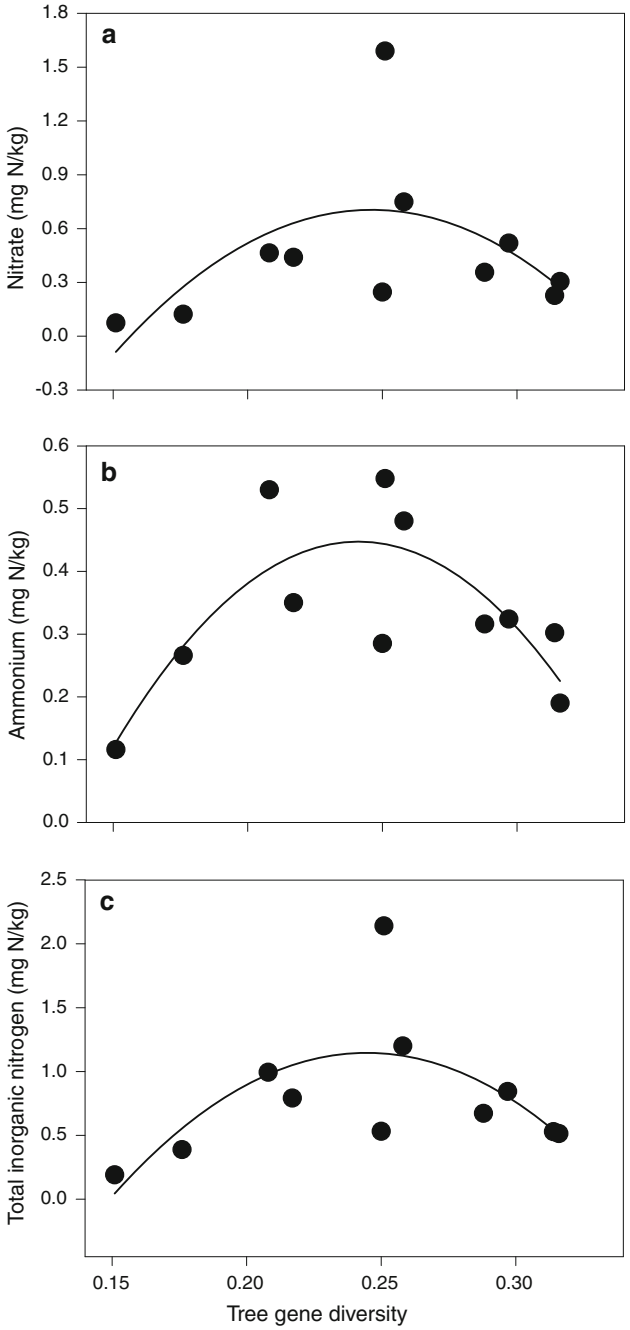

Fig. 2 Stand gene diversity (i.e., heterozygosity) is nonlinearly correlated to soil nitrogen (N) availability, as determined from in situ ion-exchange resin bags. The availability of NO_3^- (**a**), NH_4^+ (**b**), and total inorganic nitrogen (**c**) is related to gene diversity, such that stands with intermediate gene diversity have the highest available soil N

communities and soil nutrient pools. Second, soil microbial communities respond differently than foliar arthropod communities to plant genetic variation. Third, these data confirm that plant secondary chemistry—a suite of traits often under genetic control—and the composition of the microbial community likely mediate some plant–soil interactions, which has implications for our understanding of the consequences of plant trait evolution for ecosystem function.

Genetic variation

Significant quadratic correlations between many of the studied soil microbial and soil nutrient pool data (Table 1; Fig. 1) and stand gene diversity follow patterns that are commonly found in biodiversity studies. A unimodal pattern in ecosystem processes (most often primary productivity) with biodiversity allows for more species to occupy a "local" environment until a point when multiple species overlap in their niche requirements, resulting in a reduction in function (Mittelbach et al. 2001; Bond and Chase 2002; Chase and Leibold 2002). Similar observed patterns with gene diversity may be due to the same general mechanisms. In this study, we examined gene diversity across two *Populus* spp. and their natural hybrids; therefore, we examined genotypic diversity on ecosystem processes, albeit at a finer scale than most studies. Because *P. angustifolia*, *P. fremontii*, and their hybrids (and genotypes within these crosstypes) exhibit up to 10-fold differences in productivity (Lojewski et al. 2009), root production (Fischer et al. 2006, 2007), physiology (Fischer et al. 2004), and foliar chemistry (Bailey et al. 2006; Rehill et al. 2006), differences in niches among the trees could result in the same unimodal patterns. Furthermore, because we observed these patterns at an inter- and intraspecific scale, these data suggest that the species diversity literature may also be measuring intraspecific genetic variation and/or specific functional traits (Diaz et al. 2004). Further experimentation is warranted to elucidate this hypothesis.

Specific functional traits that are responsible for documented patterns such as unimodal responses are unclear, and a more complex model including foliar secondary chemistry and microbial community composition was significant in accounting for patterns in soil NH_4^+, but not any of the other response variables that were correlated with gene diversity. These data suggest that further experimentation and analyses of microbial community responses to suites of plant phenotypic measurements will be required to better understand controlling mechanisms (Gessner et al. 2010). The combined regression model incorporating gene diversity, CTs, and microbial community composition indicated a significant relationship between plant foliar chemistry and the composition of the microbial community, which suggests that plant traits directly or indirectly may influence the composition of soil microbial communities and supports the concept that there are functional differences between microbial communities (Reed and Martiny 2007; Strickland et al. 2009; M.D. Madritch and R.L. Lindroth, unpublished data). The lack of covariance

between soil microbial community composition and the availability of other soil nutrient pools (as mediated by plant traits) does not necessarily indicate that a relationship between these factors does not exist, merely that our measure of microbial community composition may not have the resolution to detect these patterns (Zak et al. 2006). Moreover, our analyses may not have included plant functional traits that were related to these response variables (e.g., foliar lignin, plant productivity, or other soil biotic and abiotic factors). Variation in tree productivity is one hypothesis that may fit this unimodal model (Mittelbach et al. 2001; Tilman et al. 2001; Chase and Leibold 2002) and may be an important mechanism explaining many of the patterns we observed here; for example, higher productivity in intermediate gene diversity sites could result in variable microbial communities, higher fungal biomass (i.e., lower bacteria-to-fungi ratios) found in these soils, and increased activity of C-degrading exoenzymes (Fig. 1) due to increased C in the litter layer. Variation in microbial responses such as this may also result in (or be a result of) altered N availability, such as we observed in our study as well as has been found in other studies (Fig. 2; Saiya-Cork et al. 2002).

Soil communities

These results also indicate that soil microbial communities respond to variation in tree genetic composition in a very different manner from the previously published patterns correlating the same tree genetic factors with foliar arthropod communities (Wimp et al. 2004). Rather than a linear pattern between community composition and stand gene diversity, we found unimodal relationships between microbial community composition (and other soil response variables) and stand gene diversity (Figs. 1, 2). While spatial, temporal, and scaling factors controlling the diversity of arthropods compared with soil microorganisms are very different, recent studies show that microbial communities can be structured by the same ecological factors that also shape plant and animal communities. Elevation, latitude, primary producer productivity, and soil pH gradients have all recently been shown to impact broad communities of soil microorganisms (Horner-Devine et al. 2003; Fierer and Jackson 2006; Fierer et al. 2009); for example, microbial communities demonstrate unimodal patterns correlated with productivity gradients in experimental microcosms (Horner-Devine et al. 2003) and also demonstrate strong correlations with soil pH (Fierer and Jackson 2006; Fierer et al. 2009). The data reported here indicate that soil microbial communities and the nutrient processes that they mediate (i.e., organic matter decomposition, ammonification) may be influenced by plant genetic traits (sensu Schweitzer et al. 2008a; Madritch et al. 2009; M.D. Madritch and R.L. Lindroth, unpublished data) that also follow a unimodal distribution, whereas arthropod communities are structured by other, unknown phenotypic traits and have a more intimate, direct relationship with the host plant. For example, studies in *Pinus edulis* in western USA have found differential responses to a stress gradient between soil microbial communities (mycorrhizal colonization) and foliar arthropod communities. Swaty et al. (2004) showed that, along a drought-stress gradient, mycorrhiza exhibited a unimodal pattern in which colonization was highest at intermediate stress/productivity levels; however, on the same trees, Stone et al. (2010) showed that arthropods decreased linearly.

Studies examining the role of plant genetic variation on above- and belowground communities have found that soil communities can sometimes display more idiosyncratic patterns than aboveground communities (Crutsinger et al. 2008; Barbour et al. 2009b); for example, Crutsinger et al. (2008) found that litter-based microarthropod communities show weak effects of plant genotype and genotypic diversity compared with foliar herbivores (and other guilds) that show strong responses to genotype (Crutsinger et al. 2006). In contrast, litter arthropods (at early stages of decay) and canopy arthropods are both affected by tree provenance-level genetic divergence within *Eucalyptus globulus* (Barbour et al. 2009b). Variation in study design and genetic scale make these studies difficult to compare directly; however, they indicate that much more study is required to understand the strength and reach of plant genetic variation in structuring the communities of associated species on foliage and in soil (or across habitat types, LeRoy et al. 2006).

Plant traits

Plant traits, such as secondary chemistry, appear to be an important link between plant genetic variation and soil communities and the nutrient cycling processes they mediate. We found that CT was a significant plant trait that directly mediated soil NH_4^+ availability (but was not related to other soil factors). Condensed tannins (proanthocyanidins) are complex flavonoid polymers produced by plants that influence mammals, arthropods, microorganisms, and ecosystem processes (e.g., nitrification), and provide mechanisms for detrital linkages between plants and soils. In many plant species, CTs have been shown to influence microorganisms (Scalbert 1991) and alter mycorrhizal interactions (Bending and Read 1996; Northrup et al. 1998). In turn, these effects (especially on heterotrophic microorganisms) may alter rates of leaf litter decay (Basaraba and Starkey 1966; Horner et al. 1988) and nutrient mineralization (Schimel et al. 1996; Northup et al. 1998; Nierop et al. 2006), thus influencing overall nutrient

availability within ecosystems (Hättenschwiler and Vitousek 2000; Kraus et al. 2003). We found that CTs were important to NH_4^+ availability but not to any of the other factors significantly related to stand gene diversity, although in previous studies with *Populus* spp. CTs have been highly correlated to rates of leaf litter decomposition, nutrient mineralization, and trophic dynamics (Schweitzer et al. 2004, 2005, 2008b; Bailey et al. 2006). Nitrifying bacteria may be more sensitive to other plant traits or other community members that were not captured in these analyses.

Conclusions

While there is a growing literature on the various ways that plant genetic variation [i.e., expressed as genotypic variation, genotypic diversity, allelic/nucleotide diversity, genetic variance (V_G)] can impact the community structure of associated species and directly or indirectly impact ecosystem processes (Hughes et al. 2008; Bailey et al. 2009), the role of forest genetic diversity on soil communities and soil processes is less explored, particularly in natural field conditions (but see Madritch et al. 2009). However, plant genotype, in both experimental common garden and natural field conditions (i.e., aspen clones across the landscape), has been shown to vary strongly in a multitude of plant traits that have strong effects on associated microbial communities, microbial pools of nutrients, and microbial activities (i.e., extracellular enzyme activity; Schweitzer et al. 2008a; Madritch et al. 2009; M.D. Madritch and R.L. Lindroth, unpublished data). These genotypic differences in plant traits also directly and indirectly impact leaf litter decomposition and mineralization processes in soil organic matter (Schweitzer et al. 2005, in press; Madritch et al. 2006; Crutsinger et al. 2008, 2009). Moreover, when genotypes are grown in mixtures, they can demonstrate nonadditive patterns of total productivity (Crutsinger et al. 2006), which may in turn have effects on soil nutrient availability. Data such as reported here across a natural hybridization gradient indicate that genetic variance across a gradient of gene introgression can result in strong patterns of trait variance that are correlated with associated soil communities and soil available nutrients. Neutral genetic variance (i.e., from AFLP markers) is likely only indicative of overall variance in plant functional traits and confirms patterns found across this gradient in the past (i.e., that strong phenotypic variance exists among *P. fremontii*, *P. angustifolia*, and their hybrids) that can have significant ecological effects on associated species and ecosystem processes (Whitham et al. 2003, 2006) with fitness consequences (Pregitzer et al. 2010).

We conclude that forest gene diversity may alter soil microbial communities and their activities, which may have extended consequences for soil fertility. Moreover, these data suggest that stand gene diversity results in similar unimodal patterns to species diversity, indicating that intermediate levels of genetic diversity may commonly have large effects on some ecosystem processes. Explicit tests of the role of genetic variation in species variation studies as related to ecosystem processes are long overdue (but see Crutsinger et al. 2009; Wardle et al. 2009). This study examined genetic variation across a species hybridizing gradient and provided a rare look at how genetic variation across closely related species may alter community dynamics and ecosystem processes. The results suggest that specific factors that determine functional gene expression for key traits may be more important to predicting community and ecosystem phenotypes than species or genetic variation per se.

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