

Evidence for indirect effects of plant diversity and composition on net nitrification

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Abstract Abiotic controls on net nitrification rates are well documented, but the potential effects of plants on this important ecosystem process are poorly understood. We evaluated four structural equation models to determine the relative importance of plant community composition, aboveground herbaceous production, and plant species richness on nitrifier abundance and net nitrification following restoration treatments in a ponderosa pine forest. Model selection criteria indicated that species richness was the best predictor of nitrifier abundance, but a model that included community composition effects also had some support in the data. Model results suggest that

net nitrification was indirectly related to plant species richness via a positive relationship between species richness and nitrifier abundance. Community composition was indirectly related to nitrifier abundance through its relationship with species richness. Our model indicates that species-rich plant communities dominated by C_3 graminoids and legumes are associated with soils that have high abundances of nitrifiers. This study highlights the complexity of deciphering effects of ecological treatments on a system response when multiple interacting factors are simultaneously affected. Our results suggest that plant diversity and composition can both respond to forest thinning, prescribed fire and fuel manipulations, and can be factors that might indirectly influence an ecosystem process such as nitrification. Ecological restoration treatments designed to increase plant diversity and alter community composition may have cascading effects on below-ground processes.

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Introduction

Understanding ecosystem functioning requires approaches that can unravel the complex interactions and feedbacks between plant communities and below-ground processes (Wardle 2002). One such process,

the internal cycling of nitrogen (N), is a critical function for terrestrial ecosystems because it accounts for about 88% of the global N demand of plants (Schlesinger 1997). This process includes the mineralization of organic N to ammonium, the oxidation of mineralized ammonium to nitrite and nitrate (nitrification), the microbial assimilation of these mineral forms of N by microorganisms, and plant uptake (Hart et al. 1994). The major abiotic controls on nitrification are well documented (Robertson and Groffman 2007), but less is known about biotic factors such as the above-ground plant community that may also influence this important ecosystem process. In this study, we evaluate the relative significance of community composition, herbaceous production, and plant species richness to net nitrification in an applied context of forest restoration, where changes in ecosystem functioning are of great concern (Kaye and Hart 1998).

Southwestern ponderosa pine forests have become increasingly dense over the last century due to fire suppression, logging, grazing, and favorable climatic events for pine regeneration (Covington et al. 1997). These changes in forest structure have led to a decline in understory production and diversity (Moore et al. 2006; Laughlin et al. 2008) and have reduced nitrogen transformation rates in the soil (Kaye and Hart 1998). In 1992, a long-term restoration experiment was initiated to understand the effects of tree thinning and prescribed burning on forest structure and ecosystem function (Covington et al. 1997). Nitrogen transformation rates responded positively to the treatments and was thought to be in response to increased herbaceous plant production in the understory (Kaye and Hart 1998; Moore et al. 2006). The patchy distribution of trees combined with the thinning and burning treatments created variation in plant diversity, community composition, and herbaceous productivity across the study site, thereby providing an opportunity to compare the influences of these three properties of the plant community on the key ecosystem process of nitrification.

Any effect of plants on nitrification rates must be mediated by their effects on nitrifying microorganisms (Wardle 2002). Nitrifiers in this system are likely mostly chemolithotrophs, given the circum-neutral pH of the soil, which obtain carbon from carbon dioxide and obtain energy from oxidizing ammonium and nitrite (Robertson and Groffman 2007). Any effect of

plant diversity or composition on nitrifiers is likely mediated through ammonium availability (Kaye and Hart 1997). Ammonium availability could be influenced by three attributes of the plant community: composition, productivity, or diversity. First, the composition of the plant community could influence ammonium availability because a community dominated by plants with high nitrogen concentrations would likely have positive effects on mineralization rates (Grime 1998). Previous work has shown that the quality of plant material can determine the structure of microbial communities (Bardgett et al. 1999; Griffiths et al. 1999; Hart et al. 2005) and chemical compounds present in certain plants can inhibit nitrifier activity (Lodhi and Killingbeck 1980). Second, productivity could also influence ammonium availability because greater inputs of herbaceous plant material could increase mineralization rates and because soil microorganisms have been shown to respond to increased carbon and nitrogen resources exuded in the rhizosphere (Denton et al. 1999; Mikola et al. 2000). Third, ammonium availability could also be affected by plant diversity because a more diverse array of plant compounds entering the soil through leaf litterfall, root turnover, and root exudates could affect mineralization rates by providing a consistent long-term supply of organic nitrogen as the different qualities of plant material break down at different rates over time. Plant diversity has been shown to be positively related to N mineralization (Zak et al. 2003; West et al. 2006), microbial biomass (Spehn et al. 2000; Stephan et al. 2000; Zak et al. 2003), and N retention (Tilman et al. 1996). However, idiosyncratic or negative responses of ecosystem processes to plant diversity have also been detected (Wardle et al. 1999; Niklaus et al. 2001; Schmid et al. 2002; Carney et al. 2004). Clearly, determining the relative importance of plant identity, productivity, and diversity to N cycling should be an active area of research.

We developed four competing structural equation models (SEM) that represent hypotheses about above- and below-ground interactions (Fig. 1) in a recently restored ponderosa pine (*Pinus ponderosa* Laws. var. *scopulorum* Englem.) forest in northern Arizona (Kaye and Hart 1998). The “identity effects” model states that only the composition of the plant community directly influences nitrifiers and nitrification. The “production effects” model states that only production directly influences nitrifiers and net nitrification. The

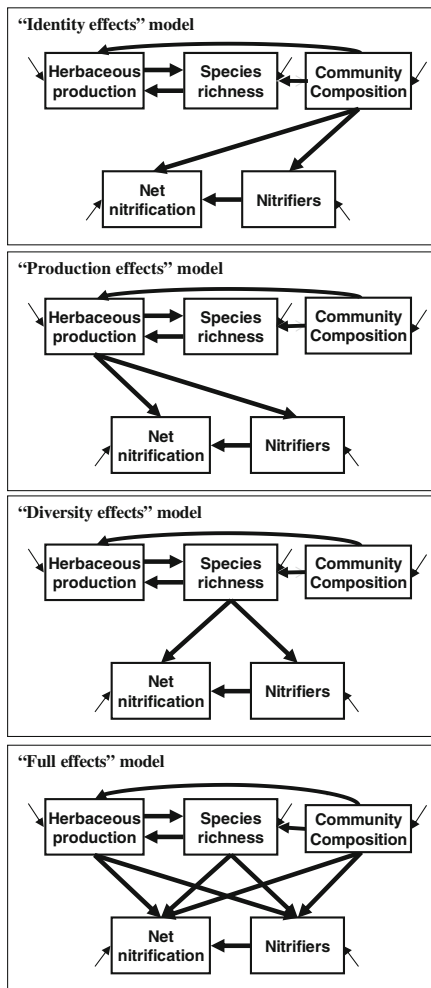


Fig. 1 Four competing models representing plausible multivariate hypotheses that relate the plant community to internal nitrogen cycling. *Small arrows* acknowledge that other factors (e.g., pine density, prescribed fire, O horizon mass, and soil carbon to nitrogen mass ratio) will be accounted for in model assessment, but these pathways do not change across the four models

“diversity effects” model asserts that only richness directly influences nitrifiers and net nitrification. The “full effects” model allows for all three factors to influence nitrifiers and net nitrification. In all models, herbaceous production and richness were allowed to influence each other simultaneously (Gross and Cardinale 2007), and herbaceous biomass and species richness were modeled as functions of community composition (Fig. 1). Pathways from abiotic factors are not shown in Fig. 1 because they do not change across models. Through these analyses, we show that the data support a model where plant diversity and

community composition may indirectly influence net nitrification through a positive relationship with nitrifier abundance, suggesting that restoration treatments designed to increase plant diversity may have cascading effects on below-ground processes.

Materials and methods

Study system

This study was conducted in a ponderosa pine forest at the Gus Pearson Natural Area (GPNA), located 10 km northwest of Flagstaff, Arizona, USA, in the Fort Valley Experimental Forest. In 1992, 55 permanent plots were established within the full spectrum of overstory canopy cover ranging from completely open to closed (Covington et al. 1997; Kaye and Hart 1998). These plots were nested within treatment plots (0.2–0.3 ha) that were either thinned, thinned and burned, or were left as controls; thus, 20 of the 55 plots were burned (Moore et al. 2006). Consequently, fire and ponderosa pine density are orthogonal factors in this study. Prior to burning in October 1994, the Oa (humus) and Oe (fragmented) layers were removed from the thinning and burning treatment plots, and approximately 67 g m^{-2} of native grasses and forbs were added to the Oi layer (last 2–4 years of pine litterfall). This native “hay” was added to emulate pre-EuroAmerican settlement fuel conditions, which supported frequent, low-severity surface fires (Covington et al. 1997). At this time of the study (1995), the thin and burn treatment had been treated only once in 1994. Prescribed fire is treated as a binary experimental factor and in lieu of modeling “thinning” effects as a binary factor, we used pine basal area to understand the effects of overstory density on other system components.

We sampled the herbaceous vegetation in September of 1995 (Moore et al. 2006). The data was collected 2 years after the initial thinning treatment but only 1 year after the first prescribed burn. Annual precipitation was near average in 1995. We determined plant species richness within 2 m^2 quadrats and harvested the peak above-ground herbaceous standing crop. Prior to weighing, plant biomass was separated into four functional types: legumes, non-leguminous forbs, C_3 graminoids, and C_4 graminoids (Moore et al. 2006). Peak above-ground herbaceous biomass is a reasonable

approximation of above-ground herbaceous net primary production (ANPP) in this ecosystem because the study area was fenced to exclude large grazers (i.e., domestic livestock, deer, and elk; Bonham 1989).

Overstory density was estimated using ponderosa pine basal area ($\text{m}^2 \text{ha}^{-1}$) on all trees within a 10 m diameter plot centered on the herbaceous quadrats. Continuous variation in pine basal area was used to estimate effects of the pine overstory on understory herbaceous vegetation and net nitrification. We also collected, dried, and weighed the surface organic horizon (O horizon) from within sampling frames at each plot; dry weights were corrected for mineral content via loss-on-ignition.

Soil organic matter was determined by mass loss-on-ignition (550°C for 6 h), and total carbon (C) was estimated using the ratio of 1.724 g organic matter/g C (Nelson and Sommers 1982). Soil total N (organic + ammonium) was determined by modified micro-Kjeldahl digestion (Parkinson and Allen 1975) and flow injection analysis using the salicylate method (Lachat Instruments 1992).

We measured seasonal rates of net nitrification *in situ* in each of the 55 plots using modified resin-core incubations (Binkley and Hart 1989) described in detail and reported in Kaye and Hart (1998). Net nitrification was calculated as the difference in soil (0–15 cm mineral soil and O horizon) nitrate pool size between incubated and initial soil plus nitrate adsorbed on the underlying resin bag. These measurements were carried out from May 1995 through April 1996 using 2–6 month incubation periods (i.e., winter and summer). Shorter incubation times (1 month to 2 months) using the cover-core incubation method (Hart et al. 1994) provide seasonal net rate estimates similar to those using resin-cores and longer incubation periods in these ecosystems (Hart et al. 2006). Though some nitrification has been shown to be caused by soil fungi (Laughlin et al. 2008), we assume that most nitrification in the soils we studied is autotrophic given the circum-neutral pH of the soils (Hart et al. 1994).

We estimated nitrifier abundance using the soil slurry method (Belser 1979; Hart et al. 1994) on soils sampled from the upper 15 cm of the mineral soil in August 1995, when we expected nitrifier activity to be at a maximum because of warm and moist soil conditions during this period (Kaye and Hart 1998; Hart et al. 2005). Briefly, soils were added to a neutral

pH, phosphate- and ammonium-rich solution. Soil slurries were shaken on an orbital mixer, and samples were drawn at 2 h, 4 h, 22 h and 24 h, and analyzed for nitrate on an autoanalyzer. The slope of the best fitting line between the four sampling periods yields an estimate of nitrate production per unit time. We relate this index of nitrifier population size to net rates of nitrification under the assumption that relative abundance of nitrifiers will be similar among different canopy types throughout the growing season; this assumption has previous empirical support (Davidson et al. 1990).

Data analysis

We quantified the composition of the plant community using non-metric multidimensional scaling (NMS; McCune and Grace 2002). We used the standing crop of four functional types (legumes, non-leguminous forbs, C_3 graminoids, and C_4 graminoids) as response variables. We used the Bray-Curtis distance measure with random starting configurations, 50 runs with real data, a maximum of 250 iterations per run, and a stability criterion of 0.00001. A Monte Carlo test with 50 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone. The final stress for the three-dimensional solution was 7.4 ($P=0.0196$). We rotated the final configuration to maximize the covariance between the first ordination axis and nitrifier abundance in order to maximize the possibility that composition is related to nitrification. The scores for each plot along the first NMS axis were used in the structural equation model analysis to represent community composition. The first NMS axis was positively correlated with the abundance of C_3 graminoids and legumes.

We compared four SEMs to determine the relative importance of community composition, species richness, and herbaceous production effects on nitrifier abundance and net nitrification after accounting for important abiotic factors. The four models in Fig. 1 highlight the mechanistic differences between the models without illustrating the remaining pathways from abiotic factors, which are constant across the four models.

All four models included the hypotheses that net nitrification is a function of: 1) nitrifier abundance; 2) the relative availability of C and N in the soil,

measured by the soil C:N mass ratio (Robertson and Groffman 2007); 3) O horizon mass; and 4) ponderosa pine basal area. The O horizon and pine basal area negatively influence soil temperature and soil moisture, respectively, primarily through shading and evapotranspiration (Hart et al. 2005). However, we could not include soil moisture and temperature directly in the model since these data were only measured on 22 out of 55 plots. The mean maximum soil temperature in 1995 was negatively correlated with O horizon mass ($n=21$, $r=-0.55$, $P=0.0091$), and mineral soil moisture during the summer monsoon season was negatively correlated with pine basal area ($n=55$, $r=-0.37$, $P=0.0053$).

We used observed variable SEM, which includes only variables that have been directly measured (Grace 2006). We used maximum likelihood to estimate model parameters using Mplus software (Muthén and Muthén 2005). Structural equation modeling allowed us to quantify simultaneous feedbacks among model components. Recent analyses suggest that plant diversity and productivity may influence each other simultaneously (Gross and Cardinale 2007). Therefore, evaluations of statistical models that allow for reciprocal relationships are essential for clarifying our understanding of natural systems (e.g., Grace et al. 2007), especially when assessing the relative importance of diversity and productivity to N cycling rates. Nonrecursive models involve direct feedback where two variables are in a reciprocal relationship within one sampling period. This method requires that the model is sufficiently identified to obtain a unique solution, and that the processes being sampled are occurring simultaneously (Grace 2006). Following the reasoning outlined by Grace et al. (2007), we used this technique to evaluate the relationships between herbaceous production and herbaceous species richness (Fig. 1).

We used the second-order bias corrected Akaike Information Criterion (AICc) to evaluate the support for the four models (Burnham and Anderson 2002). The AICc value for each model was rescaled to Δ_i by subtracting the smallest AICc in the model set from the other AICc values. The resulting Δ_i values were then converted to Akaike weights (w_i), which sum to 1 and can be interpreted as the weight of evidence in favor of model i .

Because any model selection criterion can potentially select poor models if no good model is in the

candidate set, we also employed the chi-square goodness of fit measure to ensure that there were no model-data discrepancies in the model with most support. Models that fit the data have small chi-square values and large P -values, suggesting that the covariance structure of the model is consistent with the covariance structure of the data. In the final selected model, a composite variable was used to model quadratic relationships (Grace 2006). Squared terms are not illustrated in the model figures for simplicity in data presentation, but quadratic relationships are indicated by (\pm). We used logarithmic (base e) transformations of pine basal area, O horizon mass, and net nitrification to eliminate heteroscedasticity within bivariate relationships.

We further evaluated the relationship between plant communities and nitrification using multiple regression analysis. The first model regressed nitrifier abundance on soil C:N ratio, plant species richness, and the non-metric multidimensional scaling (NMS) ordination axis. The second model regressed nitrifier abundance on soil C:N ratio, plant species richness, and peak standing crop of four functional groups (legumes, non-leguminous forbs, C_3 graminoids, and C_4 graminoids).

Results

Bivariate scatterplots illustrate relationships between above-ground plant community attributes and below-ground soil attributes. First, nitrifier abundance was positively related to community composition, herbaceous production, and species richness, and negatively related to the soil C:N ratio (Fig. 2a–d). Second, net nitrification rates were negatively related to the soil C:N ratio and pine basal area, positively related to herbaceous production and species richness, and nonlinearly related to nitrifier abundance (Fig. 2e–i). Third, herbaceous production was a positive function of plant species richness and a negative function of pine basal area (Fig. 3a–b). Fourth, species richness was a nonlinear function of herbaceous production, and was positively correlated with the NMS ordination axis (Fig. 3c–d). Given that ecological theories predict that richness is a nonlinear function of production and that production may be a positive function of richness, the reciprocal relationships between them must be simultaneously evaluated using a nonrecursive SEM.

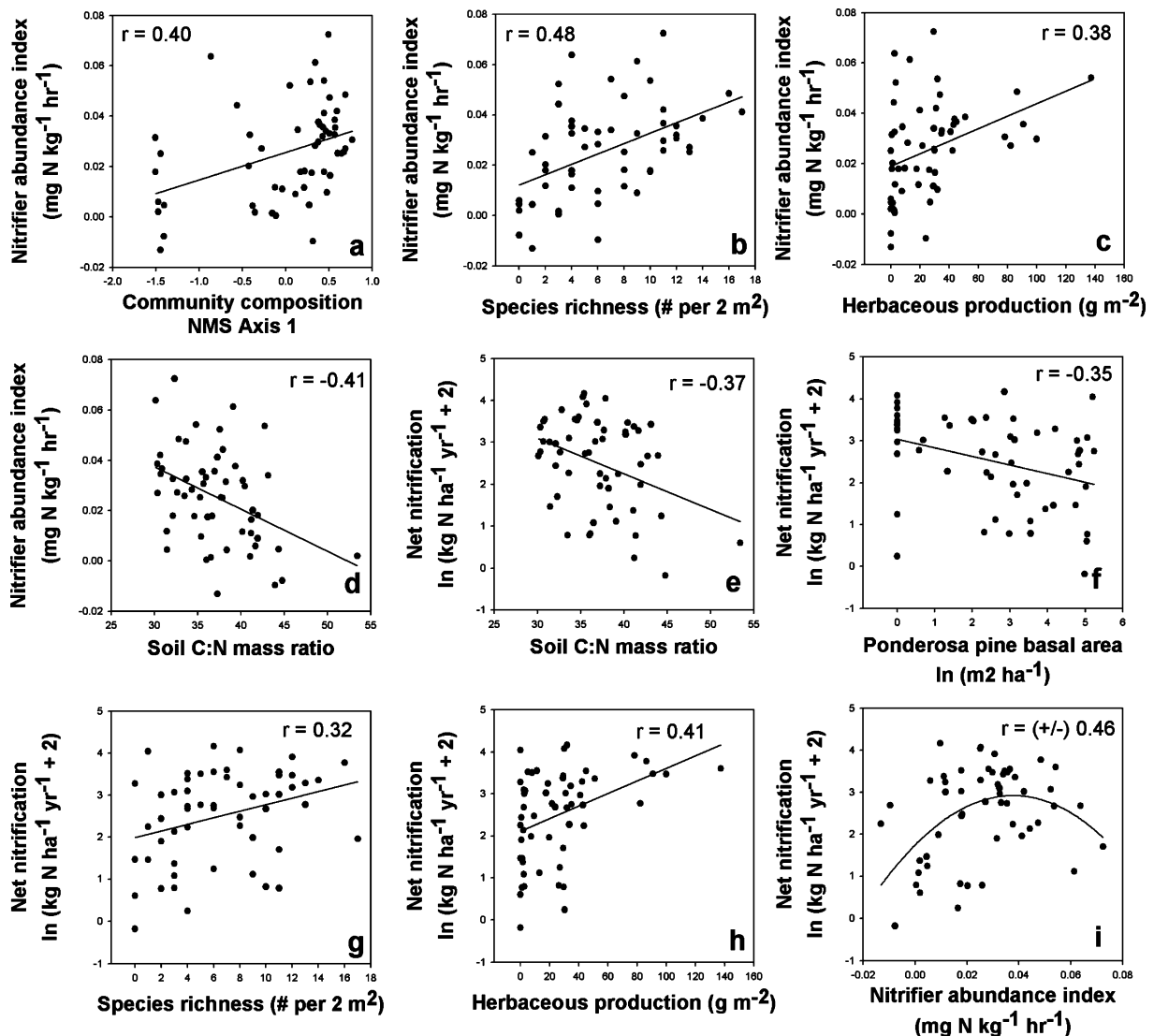


Fig. 2 Bivariate relationships between nitrifier abundance (a–d) and net nitrification (e–i) and the factors proposed to influence each in a ponderosa pine forest. Nitrifier abundance

was estimated using the method of Belser (1979) and Hart et al. (1994). Soil C:N ratio = mineral soil carbon to nitrogen mass ratio

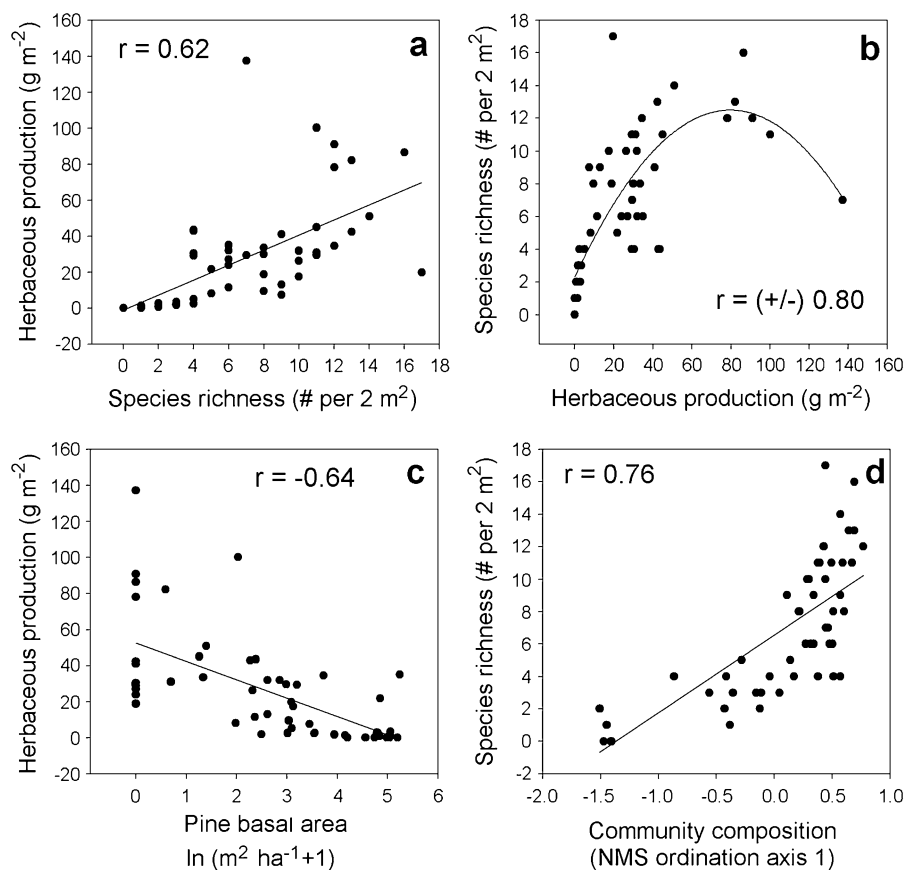
No model received overwhelming support in the data. Model selection criterion (AICc) suggested that the “diversity effects” model was the most likely of the four models, given these data (Table 1). The “diversity effects” model was 2.8 times more likely than the “identity effects” model and was 7.8 times more likely than the “production effects” model (Table 1). The “production effects” and “full effects” models received little support in the data. Given that the diversity effects model received the most support, we show parameter estimates for this model in Fig. 4. The diversity effects model yielded

no significant model-data discrepancies ($\chi^2=36.4$, 27 df, $P=0.11$).

The selection of the diversity effects model implies that net nitrification was indirectly linked to herbaceous plant species richness through the mediating effects of nitrifier abundance, and community composition was indirectly linked to nitrifier abundance through its relationship with species richness (Fig. 4). After accounting for covariates, species richness and herbaceous production were uncorrelated (Fig. 4).

Multiple regression analyses were used to further explore whether richness or composition was more

Fig 3 Bivariate relationships between species richness and above-ground herbaceous production (**a** and **b**), between herbaceous production and pine basal area (**c**), and between species richness and community composition as represented by axis scores on the first NMS ordination axis (**d**) in a ponderosa pine forest



strongly related to nitrifier abundance. These analyses lend additional support to the hypothesis that species richness is an important predictor of nitrifier abundance in the presence of either the NMS ordination axis or the peak biomass of the major plant functional types (Table 2). In the first multiple regression model (Table 2), the soil C:N ratio ($P=0.015$) was the most important predictor of nitrifier abundance, species richness was a marginally important predictor ($P=0.059$), and the NMS ordination axis was not an important predictor ($P=0.74$). In the second multiple regression model (Table 2), the soil C:N ratio was the most important predictor of nitrifier abundance ($P=0.015$), species richness was also a significant predictor ($P=0.039$), but none of the four plant functional types were significant predictors (each $P>0.25$).

Discussion

Our model suggests that plant diversity and community composition can simultaneously be both a

response to restoration treatments and a factor that may influence a below-ground ecosystem process. Overstorey removal through thinning small-diameter trees stimulates herbaceous production and influences community composition, and forest floor reduction through the reintroduction of surface fires increases species richness. Ecological restoration treatments that alter the composition of the plant community may therefore have cascading effects on nitrifier abundance and rates of nitrification.

Net nitrification was controlled by both abiotic and biotic factors, and was indirectly linked to herbaceous plant species richness (Fig. 4) through the mediating effects of nitrifier abundance. Net nitrification was unexpectedly highest at intermediate abundances of nitrifiers (Fig. 2). We speculate that at high nitrifier abundances a decline in net nitrification occurs because of greater amounts of microbial immobilization of nitrate relative to ammonium as available N pools become dominated by nitrate (Stark and Hart 1997).

Biotic effects on net nitrification were nearly equally as important as abiotic effects. Net nitrification was

Table 1 Model selection criteria for the four competing structural equation models using the second-order bias corrected Akaike Information Criterion (AICc). The AICc value for each model was rescaled to Δ_i by subtracting the smallest AICc in the model set from the other AICc values. The resulting Δ_i values were then converted to Akaike weights (w_i), which sum to 1, and can be interpreted as the weight of evidence in favor of each model

Model	AICc	Δ_i	w_i
Identity effects	2620.507	2.05	0.2411
Production effects	2622.559	4.10	0.0864
Diversity effects	2618.455	0.00	0.6725
Full effects	2709.25	90.79	0.0000

highest where soil C:N ratios were lowest (Fig. 2), which is consistent with the paradigm of increased availability of ammonium to nitrifiers as microbial immobilization of ammonium declines (Hart et al. 1994). High pine basal area directly reduced net nitrification rates independent of effects through herbaceous production and species richness. This may be due to allelopathic inhibition of nitrification (Lodhi and Killingbeck 1980), and can also be explained by the negative effects of evapotranspiration on soil water content as pine basal area increases (see “Materials and methods”), which strongly influences microbial activity (Robertson and Groffman 2007). After accounting for

pine basal area, O horizon mass was positively related to net nitrification rates, which was surprising given that O horizon mass reduced soil temperatures (see “Materials and methods”). We speculate that the O horizon moderated temporal fluctuations in the mineral soil microclimate (Perry et al. 2008), thereby increasing mean microbial process rates. However, prescribed fire effects on nitrification were complex and offsetting. The fire and fuel manipulation reduced the mass of the O horizon. However, the O horizon was also negatively related to species richness, suggesting that the negative fire effect on nitrification mediated through the O horizon was offset by the positive fire effect mediated through an increase in species richness. These results suggest that fire and thinning treatments may offset each other with respect to their effects on net nitrification (Kaye and Hart 1998).

Nitrifier abundance was positively associated with herbaceous plant species richness (Fig. 2), even after accounting for the negative effect of C:N ratios on nitrifier abundance (Fig. 4). It has been suggested that microbial biomass can be stimulated by diverse organic substrates (Bardgett and Shine 1999), but this is likely only true for heterotrophic microbes that obtain C from organic matter. In contrast, chemolithotrophic nitrifiers obtain energy from oxidizing ammonium and nitrite (Robertson and Groffman 2007). We suggest that the mechanistic link between

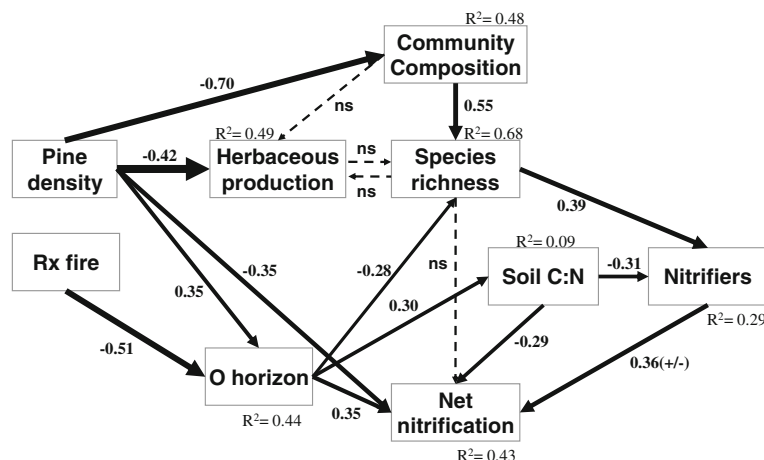


Fig. 4 Final “diversity effects” structural equation model results with standardized path coefficients ($\chi^2=36.4$, 27 df, $P=0.11$). Coefficients followed by (\pm) indicate quadratic relationships and dashed arrows indicate that the 95% confidence intervals for the coefficients overlapped with zero. Pine density = ponderosa pine basal area; O horizon = surface

organic horizon (forest floor) mass; Rx fire = prescribed fire and fuel manipulation; Herbaceous production = peak above-ground standing crop; Species richness = herbaceous species richness per 2 m²; Soil C:N = mineral soil C:N mass ratio; Nitrifiers = an index of nitrifier abundance using the method of Belser (1979) and Hart et al. (1994)

Table 2 Results of two multiple regression analyses that evaluated the relationships between nitrifier abundance and plant community composition when species richness is included in the model. This table reports the 95% confidence

intervals (point estimate \pm half interval) for the unstandardized regression coefficients. Asterisks (*) highlight the 95% confidence intervals that do not overlap with zero (indicating a significant direct relationship)

Response	Predictor	95% confidence interval
1. Nitrifier abundance	Soil C:N ratio	-0.0012 \pm 0.0010*
	Species richness	0.0015 \pm 0.0016
	NMS ordination axis 1	0.0016 \pm 0.0097
2. Nitrifier abundance	Soil C:N ratio	-0.0013 \pm 0.0010*
	Species richness	0.0017 \pm 0.0016*
	Leguminous forb biomass	-0.0001 \pm 0.0002
	Non-leguminous forb biomass	0.00002 \pm 0.0001
	C ₃ graminoid biomass	0.00001 \pm 0.00002
	C ₄ graminoid biomass	-0.00002 \pm 0.0001

plant diversity effects on nitrifiers is likely mediated through ammonium availability (Kaye and Hart 1997). A diverse array of litter quality in a community could affect mineralization rates by providing a more consistent long-term supply of organic N as the different qualities of plant material break down at different rates over time. The model also implies that the composition of the plant community can influence nitrifier abundance through its relationship with species richness. Apparently, richness has a stronger relationship to nitrifier abundance than community composition, but model results suggest that the identity of the plant community does have an effect on below-ground processes.

Herbaceous production was not the most important predictor of nitrifier abundance or net nitrification, which was surprising given that other studies have concluded that plant productivity covaries with soil microbial biomass (Wardle et al. 1999; Spehn et al. 2000). Indeed, increasing primary production increases litter inputs and root exudation and turnover, which should stimulate microbial communities (Wardle 2002). Perhaps the qualities of diverse organic substrates are more important than the quantity of detrital inputs or root exudates in this system.

It was also surprising that the functional identity of the plant community did not play a more significant role in predicting nitrifier abundance or nitrification rates. Bivariate relationships suggested that community composition was correlated with nitrifier abundance, but the importance of composition as a predictor declined in the

presence of species richness. The NMS axis was correlated with species richness such that the most diverse communities were dominated by C₃ graminoids and legumes, suggesting that the functional identity of the plant community could still be an important factor that can influence ecosystem processes (Grime 1998). Our model indicates that species-rich plant communities dominated by C₃ graminoids and legumes are associated with soils that have high abundances of nitrifiers.

Despite a recent flurry of empirical and theoretical work, there is no clear relationship between diversity and ecosystem process rates in the literature. This may be due to a variety of reasons, including differences in soil characteristics among studies and inherent differences between synthesized versus natural communities. Zak et al. (2003) detected a positive plant diversity effect on gross N mineralization at Cedar Creek, which have soils low in organic matter (4 g C kg⁻¹ to 5 g C kg⁻¹), whereas Wardle et al. (1999) detected no relationship between plant diversity and decomposition rates in New Zealand soils that were rich in organic matter (130 g C kg⁻¹). The soils in this ponderosa pine forest contain about 40 g C kg⁻¹ in the surface soil (Kaye and Hart 1998), which is intermediate but closer to those found at Cedar Creek. Perhaps the relative availability of organic C in soils mediates the relationship between plant diversity and soil microbial processes, as suggested by Zak et al. (2003). Furthermore, there is growing evidence that diversity does not strongly influence primary productivity in

natural compared to experimentally synthesized ecosystems (Grime 2001; Kahmen et al. 2005; Grace et al. 2007). Finally, it cannot be expected that diversity positively affects all ecosystem processes (Wardle 2002). It is likely that diversity effects are both process- and context-specific.

Our analysis suggests that forest restoration treatments that positively affect plant species richness and shift community composition may also indirectly influence a specific functional group of microorganisms (nitrifiers) that have strong effects on ecosystem function. Moreover, herbaceous plant species richness may be used as a predictor of nitrifier abundance following restoration treatments in southwestern USA ponderosa pine forests. This analysis represents short-term effects of restoration treatments, and future work should examine longer-term and temporal responses of below-ground processes to treatments while accounting for plant community dynamics. Although diversity was not seen to influence primary production, it may indirectly influence other ecosystem processes, such as internal N cycling, through positive effects on nitrifiers. Such plant diversity effects on N cycling may feed back to influence plant communities.

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