Responses of Redwood Soil Microbial Community Structure and N Transformations to Climate Change

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Abstract

Soil microorganisms perform critical ecosystem functions, including decomposition, nitrogen (N) mineralization and nitrification. Soil temperature and water availability can be critical determinants of the rates of these processes as well as microbial community composition and structure. This research examined how changes in climate affect bacterial and fungal community structures and rates of N mineralization and nitrification in coast redwood forest soils. Soils were reciprocally transplanted between three redwood sites located across a latitudinal climate gradient, from near the southern extent of redwoods to near their northern extent and collected one year later at the end of the summer. A molecular community fingerprinting technique was used to examine changes in fungal and bacterial community structures, and ^{15}N-isotope pool dilution was used to measure gross rates of N mineralization and nitrification. After one year, soil fungal and bacterial community structures in transplanted soils had changed to become more similar, but not identical, to those native to their new destination sites. Both climatic and edaphic variables were correlated with the variability in microbial community structure. While there were few significant differences in gross N mineralization rates between soil-climate combinations, gross nitrification rates were influenced by a change in climate. Rates of gross nitrification were highest in soils when located in the wetter, most northern site. While rates of gross nitrification varied widely in soils with water potentials above -0.05 MPa, rates were low in soils below -0.05 MPa. Changes in redwood climate, fog frequency and summer water availability will likely alter soil microbial community structure and rates of gross nitrification. Greater magnitude changes in climate or more than one year of exposure may be necessary to cause alterations in rates of gross N mineralization.

Key words: bacteria, climate change, fungi, microbial community structure, nitrogen, redwood

Introduction

Global climate models predict alterations in regional patterns of precipitation and temperature (IPCC 2007). An understanding of how soil microbes respond to alterations in climate is important because these organisms determine many aspects of ecosystem structure, function and services. While patterns have been proposed for the manner in which macrobiota can respond to shifts in climate (e.g., shifts in species range with latitude or altitude; Colwell et al. 2008, Parmesan and Yohe 2003), we have limited knowledge of microbial responses to climate change.

Due to the influence of temperature and moisture on microbial activity, changes in gross nitrogen (N) mineralization and nitrification are likely to occur in response to climate change. Soil moisture, in particular, has been suggested to be one of the main

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factors that will influence rates of soil N mineralization and nitrification in response to changes in climate, especially in seasonally dry ecosystems (Gomez-Rey et al. 2010, Jamieson et al. 1999). It is possible that N mineralization may not be as readily affected by changes in moisture as gross nitrification because N mineralization reactions are carried out by a wide variety of prokaryotic organisms and fungi while nitrification is carried out by only a limited number of archaeal and bacterial groups (Gleeson et al. 2010, Paul and Clark 1996).

This study examined the impact of climate change on rates of gross N mineralization, gross nitrification and soil fungal and bacterial community structures in coast redwood forests. Soils were transplanted across the latitudinal range of coast redwood forests in northern California to examine how interactions among native soil characteristics and changes in climatic exposure affect gross rates of N mineralization and nitrification and bacterial and fungal community structures. Soils were sampled at the end of the dry, Mediterranean-climate summer, a time of year when the presence of fog is a defining characteristic of coast redwood forests (Azevedo and Morgan 1974) and differences in fog frequency result in the most dramatic differences in temperature and soil water availability north to south. The results elucidate the potential of climate change to alter rates of these communities and important N-cycling processes, while also considering how soil characteristics can modulate the impacts of climate change.

Methods

Study sites

The three study sites were located in old-growth coast redwood forests in Prairie Creek State Park, CA (Humboldt County), the Grove of the Old Trees, Occidental, CA (Sonoma County) and Big Basin State Park, CA (Santa Cruz County), referred to as the North, Middle and South sites, respectively. The mean annual average precipitation increases with latitude and temperature decreases with latitude (*table 1*). The aboveground biomass is much greater in the North site and the rates of primary productivity and decomposition are higher there as well. Soil characteristics (e.g., soil C and N, pH, percent silt and sand, and water retention curves) also differ between the sites (*table 1*).

Experimental design: three-way reciprocal transplant

In August 2004, two types of intact soil cores (either 10 cm diameter x 15 cm deep, solid schedule 40 PVC cylinders or flexible 2 mm mesh shade cloth sown into cylinders of the same dimensions with nylon thread) were transplanted between the three sites in a full factorial design (soil from each site transplanted into every site). Five (3 m x 3 m) plots located from 30 to 400 m apart were established at each site. Plot pairs between sites were chosen randomly, and cores were randomly located within a plot. Soil cores that were returned to their plots of origin served as controls. Ninety transplanted cores were harvested after one year in early September 2005 (45 mesh and 45 PVC; five of each from three sites of origin x three transplant sites), as well as 15 previously undisturbed cores (five cores x three sites).

Table 1—*Site characteristics. See text for weather station locations for mean annual rainfall and temperature data (1970 to2000). All soil variables were measured for 0 to 15 cm, except percent C and percent N were measured for 0 to 10 cm and soil temperature was measured at 7.5 cm.*

	North	Middle	South
Location	**Prairie Creek S.P., Orick, CA**	**Grove of the Old Trees, Occidental, CA**	**Big Basin S.P., Boulder Creek, CA**
Latitude	41° 41' N	38° 24' N	37° 10' N
Distance to coast, elevation	6.8 km, 54 m.a.s.l.	6.5 km, 148 m.a.s.l.	6.4 km, 128 m.a.s.l.
Mean annual rainfall	1,677 mm	1,419 mm	1,211 mm
Air temperature, mean (range)	11 °C (2 °C – 21 °C)	14 °C (4 °C – 29 °C)	15 °C (2 °C – 30 °C)
Soil texture	Sandy Loam	Sandy Loam	Sandy Loam
Soil pH (mean +/- s.e., n=5)	4.9 +/- 0.1	5.3 +/- 0.2	5.7 +/- 0.2
Soil %C (mean +/- s.e., n=5)	10.7 +/- 0.9	4.6 +/- 0.4	4.5 +/- 0.5
Soil %N (mean +/- s.e., n=5)	0.58 +/- 0.04	0.27 +/- 0.07	0.25 +/- 0.03

Microbial community analyses

Bulk soil DNA was extracted from 500 mg of soil using the Bio101 Fast DNA Spin Kit for Soils (Q Biogene, Carlsbad, CA) according to the manufacturer's instructions. The DNA extracts were then diluted (7.5X or 10X) to approximately 40 ng / µl. The PCR primers (from Sigma-Genosys, The Woodlands, TX) used for bacteria were 27F and 1492R (Giovanni 1991), and the ITS1F and ITS4 primers, targeting the internal transcribed spacer (ITS) region of the rDNA gene, were used for fungi (Gardes and Bruns 1993). The forward primers were labeled with 6-FAM for PCR for terminal restriction fragment length polymorphism (T-RFLP; Liu et al. 1997). Three PCR reactions of each sample were bulked together before PCR clean up and digestion. All of the PCR products were purified using the MoBio UltraPure Clean Up Kit and eluted in 50 µl of elution buffer. All 10 replicates of transplanted samples and controls and five replicates of fresh undisturbed samples were analyzed by T-RFLP with bacterial primers, and four replicates (two mesh and two PVC cores for each origin-transplant combination) were analyzed for fungal T-RFLP. After PCR clean up, approximately 400 ng of bacterial 16S rDNA PCR product was digested with *MspI*. For fungi, 100 ng of fungal ITS PCR product was digested with *HhaI*. The tubes were incubated at 37 °C for 18 hours and then ethanol precipitated and washed twice before resuspension in 10 µl of fresh formamide. The abundance of different terminal restriction fragments (TRFs) was measured using an ABI 3100 capillary sequencer (Applied Biosystems, Foster City, CA) run in the GeneScan mode. Each TRF was converted into its relative abundance (percent abundance) by dividing each individual TRF peak height by the total sum of peak heights for all of the TRFs found in a sample and multiplying by 100.

Rates of gross N mineralization and nitrification

Gross rates of N mineralization and nitrification were measured by ^{15}N-isotope pool dilution (Herman et al. 1995). Soils were labeled with ^{15}N as either $(^{15}NH_4)_2SO_4$

for gross N mineralization or $K^{15}NO_3$ for gross nitrification; 1 ml of labeled solution was added to 50 g of soil to increase the appropriate pool to approximately 50 or 25 atom percent ^{15}N, respectively. Initial samples were taken after approximately 2 hours and final samples 16 hours later. Concentrations of nitrate (NO_3) and ammonium (NH_4) were determined after a one-hour extraction in 1 M KCl. Atom percent^{15}N was determined using an automated N and C analyzer coupled to an isotope-ratio mass spectrometer (ANCA-IRMS; PDZ Europa Limited, Crewe, UK) after diffusing out the NH_4 or NO_3 onto filter disks (Herman et. al. 1995). Gross rates of N mineralization and nitrification were calculated according to Kirkham and Bartholomew (1954). Soils were stored at 12 °C rates were measured at 12 °C to determine rates that were reasonably representative of field conditions (14 to 16 °C).

Climate and soil characteristics

Monthly precipitation data was obtained from NOAA National Climatic Data Center records for weather stations near each site; the stations near the North and Middle sites, respectively, were Orick Prairie Creek Park (Station 046498, 41° 22′ N and 124° 01′ W) and Occidental (Station 046370, 38° 23′ N and 122° 58′ W), and for the South, the average of Ben Lomond #4 and Felton (Station 040673, 37° 05′ N and 122° 05′ W; Station 043004, 37° 03′ N and 122° 05′ W) was used. Soil temperatures were recorded at the time of sampling and in February, May and November as well as to determine the annual ranges in soil temperature. Gravimetric water content (GWC) was determined for soils collected at the same times. Determinations of bulk density, soil particle size distributions (sand, silt, clay; Sheldrick and Wang 1993), water retention curves (Klute 1986), pH (1:1 soil:0.01M $CaCl_2$), and concentrations of soluble organic C and N (extracted in 0.05M K_2SO_4) and microbial biomass C and N (Brookes et al. 1985, Cabrera and Beare 1993) were made using standard methods. Bulk density and water retention curves were used to transform GWC into volumetric water content (VWC) and soil water potential, respectively.

Statistical analyses

To examine changes in community structure, non-metric multidimensional scaling (NMDS) was used to visualize the (dis)similarity in community structure between samples (McCune and Grace 2002). In NMDS ordinations, the farther apart samples are in space, the more they differ in structure. Permutational multivariate analysis of variance (PERMANOVA) was performed to determine if the differences in structure between soil-climate groups were significant (Anderson 2001, 2005). Pair-wise differences between groups were determined a posteriori. The Bray Curtis distance was used, and the tests were done using the distance ranks. The results from the NMDS ordinations and PERMANOVA tests were compared to hypothesized general response scenarios (*fig. 1*) to determine if the transplanted redwood microbial communities had exhibited a strong response, intermediate response or no response to the change in climate. Transplanted samples were always compared to the control samples of both the site of origin and the new transplant destination.

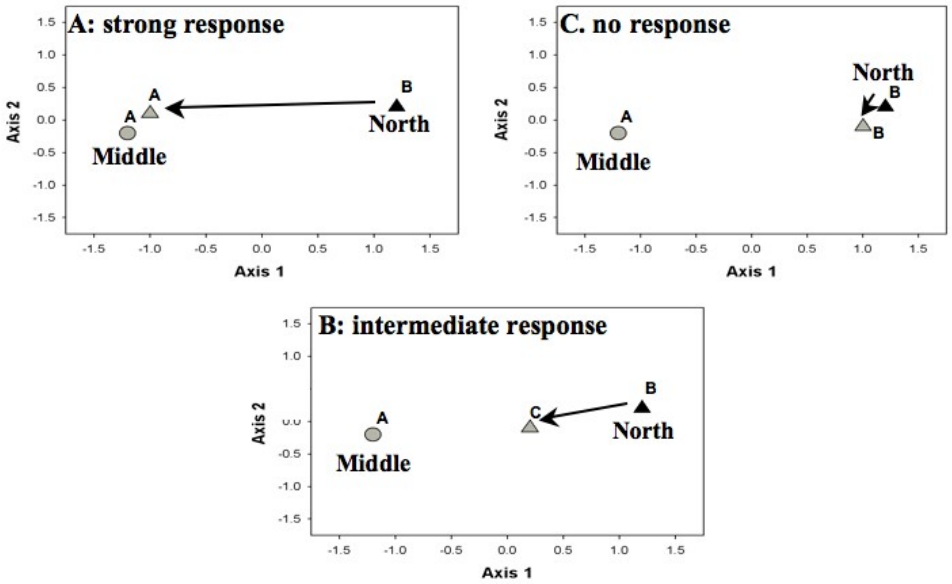

Figure 1—Hypothetical responses of soil microbial communities to climate change shown in theoretical NMDS ordinations. The distance between samples is indicative of the magnitude of their dissimilarity in community composition. Different letters indicate significant differences, as determined by PERMANOVA. The theoretical communities from the North and Middle controls are labeled and that of the North soil transplanted into the Middle climate is shown as a gray triangle.

The variability in fungal and bacterial community structure was correlated with environmental variables by performing Mantel tests. The Bray-Curtis distance was used for the taxa abundance matrix and the Euclidean distance for the environmental variable matrix. The standardized Mantel statistic (r) is equivalent to the Pearson's correlation (r) statistic. Mantel tests were performed to examine correlations between fungal and bacterial community structures and several climatic and edaphic variables, including: gravimetric water content, volumetric water content, water-filled pore space, water potential, total annual rainfall, spring rainfall (MJ), summer rainfall (JA), temperature, maximum mean monthly temperature, soluble organic carbon, total soluble nitrogen, microbial biomass carbon, microbial biomass nitrogen, pH, percent sand, percent silt and percent clay and pH.

Two-way analysis of variance was performed to determine if there were differences in gross rates of N mineralization and nitrification between sites of origin, transplant sites, or the interaction between the two (using R version 2.10.0). Because the results for the two types of cores (PVC and mesh) did not differ significantly, they were analyzed together. The N mineralization and nitrification results are presented as the averages by either the soil origins or the sites of transplantation/incubation because the interaction terms were not significant for either process rate.

Results

Effect of transplant on soil microbial community structure

In general, after 1 year, the fungal and bacterial community structures of the transplanted samples shifted to more closely resemble those of the control soils

native to the new transplant site (climate), but they did not become indistinguishable from them. All fungal community responses were classified as "intermediate" by the NMDS ordinations and PERMANOVA results (*table 2*). For the bacteria, five of the six transplanted soils changed in structure but still differed from the control samples of the new site (*table 2).* One transplant scenario did not cause a bacterial community response, North soil into the South climate.

Table 2—*Summary of changes in fungal (F) bacterial (B) and community structures in response to transplanting. Responses were determined from NMDS ordinations and PERMANOVA results, as shown in fig. 1.*

Transplant	Strong response	Intermediate response	No response
North into South	-	F	B
North into Middle	-	F , B	-
Middle into North	-	F , B	-
Middle into South	-	F , B	-
South into North	-	F , B	-
South into Middle	-	F , B	-

Correlations between community structures and environmental variables

Fungal community structure was significantly correlated with temperature, precipitation, pH and soil texture values. The strongest correlations were found with the maximum mean daily temperature (r = 0.62), the mean annual temperature (r = 0.56), the amount of summer rainfall (r = 0.56) and the total annual rainfall of the previous year (r = 0.37*; table 3*). When examining the correlations between bacterial community structure and environmental variables, measures of precipitation and soil water availability had weaker correlations (r = 0.15 to 0.20). Measures of soil texture and soil pH had correlations between 0.28 and 0.39, and total dissolved nitrogen (r = 0.18), microbial biomass nitrogen (r = 0.20) and microbial biomass carbon (r = 0.23) all had lower but significant correlations with bacterial T-RFLP community structure.

Table 3—*Significant standardized Mantel correlations (Mantel r) between fungal and bacterial community structures and environmental variables. Only significant correlations are shown, p < 0.01 for all.*

Environmental variable	Fungi Mantel r	Bacteria Mantel r
Max. temperature	0.62	-
Temperature	0.56	-
Summer rain	0.56	-
Annual rainfall	0.37	0.20
Late spring rain	0.32	0.15
pH	0.20	0.39
% sand, % silt, % clay	0.12 – 0.14	all 0.28
Total dissolved N	-	0.18
Gravimetric water content	-	0.10

Gross N mineralization and nitrification: soil and climate controls

Rates of gross N mineralization did not differ significantly by transplant site (p = 0.15) or the interaction of transplant site and origin (p = 0.10), but they did differ by site of origin (p = 0.02). The rates in soils with a South origin (4.8 ± 0.6 μg N g soil^{-1}

day^{-1}) were significantly greater than in soils of Middle origin (2.6 ± 0.5 μg N g soil^{-1} day^{-1}), and soils of North origin were intermediate (3.1 ± 0.7 μg N g soil^{-1} day^{-1}). Among all soil-climate combinations, rates of gross N mineralization ranged from (1.5 ± 0.4 to 6.4 ± 1.2 μg N g soil^{-1} day^{-1}). Rates of gross nitrification differed significantly among soils harvested from different sites (of transplantation), but not among soils from different origins or the interaction of transplant site and origin (*fig. 2*). Gross nitrification rates were higher when transplanted soils had been located in the North site compared to the other two sites (*fig. 2A*). In terms of soil origin, rates tended to increase from the South to the Middle to the North, but the differences were not significant (*fig. 2B*). There appeared to be a minimum soil water potential below which nitrification was seriously impaired (*fig. 3*). Below -0.05 MPa, rates of gross nitrification were always below 0.8 μg N g soil^{-1} day^{-1}. Above this water potential, rates varied widely, ranging between 0.0 and 9.5 μg N g soil^{-1} day^{-1}.

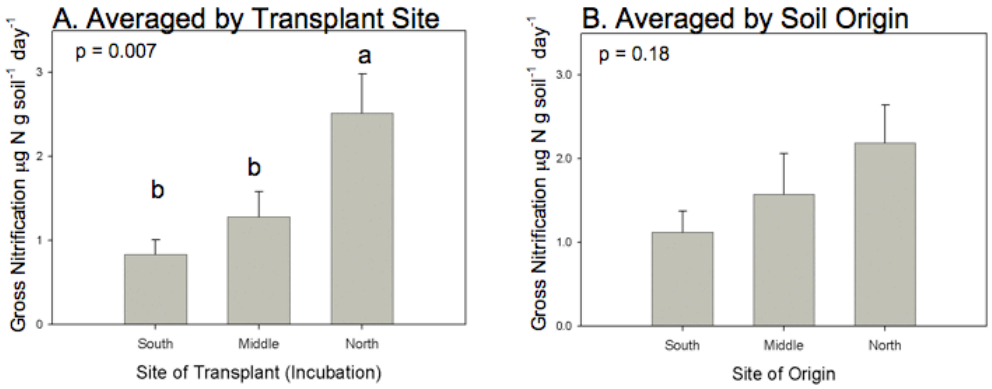

Figure 2—Gross nitrification graphed by (A) site of transplantation (incubation) and (B) site of origin for samples collected one year after transplanting. ANOVA p-values are in the upper left-hand corner and significant differences are denoted by lowercase letters. The interaction (not shown) was not significant (p = 0.32); thus, only the results averaged by site of transplantation and site of origin are shown to display the significant effect of transplantation.

Discussion

Response of bacterial and fungal community structure to a change in climate

Climate change resulting from transplanting soil cores across a 500-km latitudinal gradient in climate caused detectable changes in soil bacterial and fungal community structures within one year. Under all of the transplant scenarios, except one, the community structures of transplanted soils shifted to more closely resemble those of the sites into which they were transplanted. However, the community structures of the transplanted samples were still distinguishable from those native to their new sites. Given more time, the structure of a microbial community may

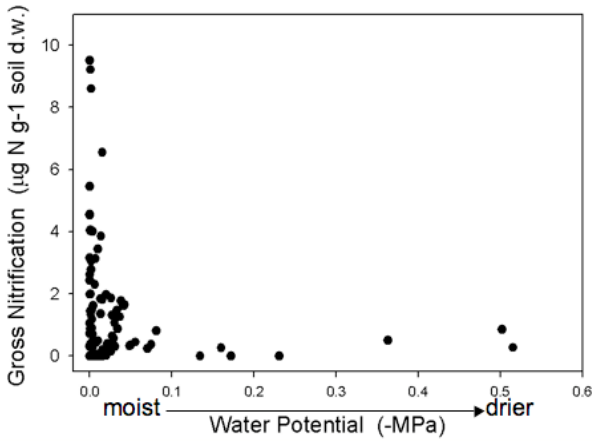

Figure 3—Rates of gross nitrification graphed against soil water potential for transplanted samples collected after 1 year.

continue to change, but it may also never fully resemble that native to the new site. While climate is clearly an important determinant of microbial community structure, it is certainly not the only significant controller.

The varying impacts of climate change on microbial community composition and structure that have been found across studies could be related to the strength of the change in climate to which soils are exposed. For example, in California, Waldrop and Firestone (2006) also found that soil microbial community structure changed when soils were transplanted from beneath oak canopies into an open grassland environment, but the reverse was not true (grassland soil microbial community structure did not change when transplanted beneath an oak canopy). They suggested that the exposure of communities to climatic conditions outside of their recently experienced range in historical climate caused a rapid change in community structure. In contrast, bacterial community composition differed little in response to increased rainfall after five years of rainfall manipulations in a coastal California grassland (Cruz-Martinez et al. 2009). However, in that study, all of the communities had experienced the same historical range in climate, one that likely encompassed the conditions experienced under the imposed rainfall manipulations. Additionally, Castro et al. (2010) observed changes in fungal and bacterial abundances and community structure after three years in response to manipulations of climatic drivers (temperature, precipitation and CO_2 concentration) in old-field ecosystems. They found that precipitation had the largest impact on community structure.

The climatic conditions of our three redwood forest sites overlap. The mean values for temperature and precipitation at all sites are within the ranges historically experienced by the indigenous communities. However, the extremes in precipitation and temperature (maxima and minima) occurring in the "new" sites post-transplanting may have provided additional stimulation for a change in community structure to occur. The warmest summer temperatures and driest soil conditions of the South site are outside of the range experienced in the North site, and the coolest winter temperatures in the North are slightly cooler than those experienced in the South. The relative importance of mean temperature and rainfall values compared to maxima and minima (and their duration) in determining differences in community composition and structure is an important but largely unexplored question.

While climate clearly influences community structure in this study, it is not the sole determinant. The predominance of intermediate changes in microbial community structure suggests that edaphic and/or biological factors also influence the trajectory and magnitude of the community response to climate. The structure of some communities may be slowly changing toward that of the new site, but in other instances, the structure of a transplanted community may never closely approach that of the new site's native community. Native soil characteristics can buffer against the effects of climate; in addition, biological interactions or environmental stochasticity could also cause the change in community structure to take a different trajectory. In this study of coast redwood soils, the strongest correlations between environmental variables and fungal community structure were found with temperature and rainfall, while bacterial community structure correlated most strongly with pH. The association of fungi with temperature and rainfall could indicate the importance of climate as a regulator of fungal decomposition, while soil pH has been found to be a strong environmental driver of bacterial community composition and structure (Chu et al. 2010, Fierer and Jackson 2006).

Impact of a change in climate on gross rates of N mineralization and nitrification

The responses of gross N mineralization and gross nitrification to imposed changes in climate differed. While rates of gross N mineralization differed somewhat among soils with different sites of origin, rates of gross nitrification differed significantly among transplant sites, that is, the sites at which the soil cores spent the preceding year (regardless of origin). Consequently, rates of gross nitrification were not correlated with rates of gross N mineralization. Instead, the impact of transplanting on gross nitrification seems to be due to the relationship between gross nitrification and water availability.

Rates of gross nitrification in coast redwood forests are clearly affected by soil water availability at the end of the summer, when north-south differences in fog frequency can cause substantial differences in climate between sites. The impacts of soil water availability on nitrification result from two primary factors: the effects of soil water content on the diffusion of NH_4 to ammonia oxidizers and the physiological impacts of the energetic availability of water (Stark and Firestone 1995). In this field study, there was a striking relationship between gross nitrification and soil water potential. Rates of nitrification were always low (< 0.8 μg N g soil^{-1} day^{-1}) below a water potential of -0.05 MPa. This water potential, however, is much greater (wetter) than the -0.6 MPa at which Stark and Firestone (1995) found physiological stress to become more important than diffusion in terms of limiting nitrification. Thus, the lower rates of nitrification below -0.05 MPa could be due to diffusional limitation of ammonium, or the ammonia oxidizers in these soils could be more sensitive to water stress since they are from a moister summer environment than the grassland soils studied by Stark and Firestone (1995). Ammonia-oxidizing bacteria are known to be able to carry out ammonia oxidation down to below -1.0 MPa in soils (Chen et al. 2011, Paul and Clark 1996), but little is known about the physiology of archaeal nitrifiers because few have been cultured (de la Torre et al. 2008, Konneke et al. 2005, Tourna et al. 2011). Soils in coast redwood forests are well suited to maintain relatively high water availability throughout the summer. The lowest water potential in this study was -0.5 MPa. The high organic matter contents (and associated high water holding capacity) and the presence of fog (which reduces

evapotranspiration) can both contribute to this characteristic. Decreases in fog water inputs could, however, lead to drier soils (Ewing et al. 2009)

In contrast to gross nitrification, rates of gross N mineralization in coast redwood forests were relatively insensitive to any variable measured, edaphic or climatic. Other studies have reported a direct relationship between gross N mineralization and substrate availability (Booth et al. 2005), and a significant relationship between gross N mineralization and concentrations of soluble organic nitrogen was previously found for two northern redwood sites (Bradbury 2011). However, that study was conducted during a very wet time of year in late winter, March 2003, while this transplant study concentrated on a drier time of year at the end of summer. At the end of the dry summer period, it may be impossible to separate substrate and water controls of gross N mineralization. Mean rates of gross N mineralization varied between ~2 and ~6 μg N g $soil^{-1}$ day^{-1} among the different origin-transplant site combinations in this study, but there was no consistent pattern in the variation of gross N mineralization among groups. Other studies conducted in pasture and grassland soils have found significant decreases in gross N mineralization at water potentials lower than those measured in these coast redwood soils (-1.5 MPa in Murphy et al. 1997 and -1.5 MPa in Jamieson et al. 1998), but a decrease in water potential from -0.1 MPa to -1.0 MPa did not cause a substantial decrease in gross N mineralization in the EA horizon of an acid coniferous forest soil (Chen et al. 2011). Thus, rates of gross N mineralization in forest mineral soils may not be highly influenced by decreases in soil water availability down to at least -1.0 MPa. Hence, greater magnitude changes in climate than those experienced in this study, or more than one year of exposure to a new climate, may be necessary to cause alterations in rates of gross N mineralization.

Implications for climate change in redwoods

Changes in summer fog frequency could have important effects on coast redwood forests. The importance of fog to coast redwood ecosystems in terms of supplying water and reducing transpiration during the otherwise dry summer has been demonstrated for coast redwood trees and their understory species (Dawson 1998, Limm et al. 2009). In this study, a regional-scale transplant-induced change in climate caused changes in fungal and bacterial community structure within one year. These changes occurred within the framework of the native soil characteristics, possibly as a result of the exposure of indigenous soil microbial communities to conditions outside of their historical range in climate. The relative importance of climate maxima and minima compared to climatic means requires further exploration. By examining the impact of differences in climate on gross N mineralization and nitrification, this study has helped to elucidate the importance of water availability for N-cycling processes that can control plant N availability at this critical time of year. While rates of gross N mineralization seem to be relatively insensitive to differences in summer climate across coast redwood forests, rates of gross nitrification are significantly affected by differences in summer climate and water availability. Therefore, continued reductions in fog frequency or amount, as have been observed over the last 100 years (Johnstone and Dawson 2010), may affect populations of ammonia-oxidizing bacteria and archaea and cause significant reductions in rates of gross nitrification and nitrate availability to redwoods and their understory species.

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