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Cross-biome assessment of gross soil nitrogen cycling in California ecosystems

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Abstract

Microbial transformations of nitrogen (N) largely determine whether N is retained in ecosystems via net primary productivity or lost via gaseous emissions and leaching. The controls on soil N cycling are often studied at single locales, making it difficult to predict N cycling at regional to global scales. We hypothesized that contemporary soil properties exhibit consistent relationships with instantaneous gross N cycling rates across diverse biomes that create a continuum in these properties. We measured ex situ gross N cycling rates and soil properties at 33 study sites representing five biome classifications in California including deserts, grasslands, shrublands, forest, and wetlands. Desert soils had significantly lower total N, organic carbon (C), microbial biomass N, and soil moisture as well as higher pH than all other biomes, whereas forests and wetlands had significantly lower soil nitrate (NO_3^-) concentrations ($P < 0.001$ for all). Gross mineralization rates were best predicted by the combination of soil moisture and soil C:N ratios ($R^2 = 0.46$), which exerted positive and negative controls, respectively. Grasslands exhibited marginally higher gross mineralization than all other biomes, whereas deserts had the lowest rates due to low soil moisture ($P = 0.09$). Gross nitrification rates were positively correlated to soil NO_3^- concentrations ($R^2 = 0.34$) and negatively correlated to soil C:N ratios ($R^2 = 0.31$). The negative relationship between gross nitrification and soil C:N ratios was driven by forest soils, which had significantly higher C:N ratios and lower gross nitrification than all other biomes ($P < 0.05$). Dissimilatory NO_3^-

reduction to NH_4^+ (DNRA) occurred in soils from all biomes. The strong positive correlation between DNRA rates and soil NO_3^- (R^2 = 0.41) suggests NO_3^- limitation of DNRA. Predictable patterns in gross N cycling across biomes in California suggest that contemporary soil properties are important drivers of instantaneous soil N cycling rates that integrate over differences in vegetation type, atmospheric N deposition rates, and local climate.

Keywords: Dissimilatory nitrate reduction to ammonium, Gross nitrogen cycling, Nitrogen mineralization, Nitrification, Nitrogen, Isotope pool dilution

1. Introduction

Nitrogen (N) is a critical nutrient that is often limiting to plants and microbes in temperate and boreal ecosystems (Vitousek and Howarth, 1991). Soil internal N cycling helps regulate the potential for N retention and loss in ecosystems. Changes in soil N cycling in response to anthropogenic N deposition and global change can lead to changes in net primary productivity (NPP), soil nitrous oxide (N_2O) emissions, and nitrate (NO_3^-) leaching into groundwater (Fowler et al., 2013; Galloway et al., 2003; Vitousek et al., 1997). Differences in soil N cycling rates have been demonstrated in crosssite comparisons of single species forest plots (Lovett et al., 2004; Zak et al., 1986), different topographic positions within a landscape (Zak and Grigal, 1991), grasslands versus forests (McKinley et al., 2008), similar ecosystems that experience a range in background N deposition rates (Rao et al., 2009) or climate (Barrett and Burke, 2000), and even different genotypes of the same species (Schweitzer et al., 2004). Despite these differences, a meta-analysis of woodlands, grasslands, and agricultural land suggested that controls on instantaneous N cycling rates are consistent across broad classes of ecosystems (Booth et al., 2005). However, desert ecosystems are also often not included in cross-ecosystem comparisons because it is assumed that limited water availability causes inherently different N cycling patterns (Amundson et al., 2003; Wang et al., 2014; Whitford and Wade, 2002). In addition, relatively few gross N cycling studies have been conducted in ecosystems with Mediterranean climates characterized by cool wet winters and hot dry summers (e.g., Davidson et al., 1992; Hawkes et al., 2005; Herman et al., 2003; Schimel et al., 1989). In ecosystems with strong seasonality in precipitation, N cycling processes may be subject to seasonally dependent controls (Mack and D'Antonio, 2003). The question remains whether the controls on instantaneous N cycling rates in arid and Mediterranean ecosystems are consistent with those in more mesic ecosystems.

Nitrogen mineralization, the process by which organic N is transformed into the inorganic form of ammonium (NH_4^+), is often considered the regulator of N availability for plant uptake. However, in ecosystems with strong N

limitation to NPP such as tundra, boreal forests, and deserts, organic N can be directly taken up by plants (Nasholm et al., 1998). Schimel and Bennett (2004) reevaluated the N mineralization paradigm suggesting that, without large exogenous N inputs, mineralization plays an increasingly important role in supporting NPP as available N becomes more abundant. A positive correlation between N mineralization rates and total available N in soils has been observed (Stanford and Smith, 1972; Wang et al., 2001), supporting this hypothesis. Mineralization can also be negatively correlated with soil C:N ratios because at high C:N ratios, microbes must immobilize rather than mineralize N to maintain the stoichiometric ratio of C:N in their biomass (Hart et al., 1994; Mack and D'Antonio, 2003). In their meta-analysis, Booth et al. (2005) found that gross N mineralization was positively correlated to total N and microbial biomass N (MBN) in soils, and negatively correlated to soil C:N after soil organic C concentration was taken into account. The meta-analysis also documented a strong positive correlation between gross N mineralization and soil moisture. Soil water can increase connectivity within the soil matrix to better distribute N among N-rich and N-poor microsites, thus increasing N abundance across microsites to support higher bulk soil N mineralization rates (Stark and Hart, 1999). Given that the microbial community in arid systems can be dominated by drought tolerant fungi that differ from bacteria in their biomass C:N ratios and response to soil moisture (Adebayo and Harris, 1971; Clark et al., 2009; Cleveland and Liptzin, 2007; Wilson and Griffin, 1975), the relationships of these soil properties to gross N mineralization rates may differ from those observed in mesic ecosystems.

Nitrification, the process by which NH_4^+ is oxidized to nitrate (NO_3^-), contributes to the potential for ecosystem N loss because NO_3^- is highly susceptible to leaching losses as well as gaseous losses to N_2O and dinitrogen (N_2) via denitrification (Robertson and Tiedje, 1987). For example, in ecosystems that receive high anthropogenic N inputs, increased nitrification is responsible for increased N leaching losses (Venterea et al., 2004). In soil microsites where there is sufficient N available to meet demands of both microbial and plant assimilation, there is likely to be N available for nitrification (Schimel and Bennett, 2004; Stark and Hart, 1999). Thus, NH_4^+ supply to nitrifiers is the proximate control on nitrification rates (Myrold et al., 1998). Indeed, Booth et al. (2005) found that gross N mineralization was the best predictor of nitrification, out of the explanatory variables evaluated. However, in ecosystems impacted by high anthropogenic N inputs that supply excess N, gross nitrification rates may be best predicted by NH_4^+ concentrations rather than gross N mineralization, which represents an internal supply of N.

Dissimilatory nitrate NO_3^- reduction to NH_4^+ (DNRA) can lead to ecosystem N retention by returning NO_3^- to the less mobile form of inorganic N, NH_4^+. This process decreases ecosystem N losses through leaching and gaseous N_2O and N_2 emissions via denitrification (Silver et al., 2001; Templer et al., 2008). Like denitrification, DNRA occurs under anaerobic conditions when N-oxides (NO_3^- and nitrite, NO_2^-) rather than oxygen (O_2) serve as terminal electron acceptors to yield energy in microbial metabolism. As such, DNRA has been documented as an important fate of NO_3^- in anoxic sediments (Bernard et al., 2015; Giblin et al., 2013; Smith et al., 2015) as well as upland soils that experience anoxic conditions (Huygens et al., 2007; Silver et al., 2001). While some studies have reported DNRA rates in non-flooded, upland soils, DNRA is rarely considered in the terrestrial N cycle (Rutting et al., 2011). The few studies that have quantified both DNRA and denitrification rates in upland soils have shown that DNRA rates can be comparable to or even many times greater than denitrification rates (Chen et al., 2015; Huygens et al., 2007; Rutting et al., 2011; Silver et al., 2001; Templer et al., 2008; Yang et al., 2015). However, to date, few studies on DNRA have been conducted in terrestrial ecosystems. Questions, therefore, remain regarding environmental controls on DNRA and how widespread this process is across bioclimatic zones and soil types.

Here, we present a survey of soil properties and gross N cycling rates in ecosystems from a wide geographical range in California, USA. We classified the ecosystems into five broad biome groups: deserts, forests, grasslands, shrublands, and wetlands. Our goals were to: (1) determine the range of gross N cycling rates across a wide range of ecosystems including arid and Mediterranean climates, and (2) determine if there are consistent relationships between soil properties and gross N cycling rates across biomes. We hypothesized that, while arid and Mediterranean ecosystems would differ in their soil properties compared to mesic ecosystems (Gallardo and Schlesinger, 1992; Post et al., 1985; Wang et al., 2014), contemporary soil properties would exhibit consistent relationships with instantaneous gross N cycling rates across these diverse biomes that create a wide continuum in these properties. Thus, we expected that differences in N cycling rates across biomes would be driven by differences in soil properties. If other factors, such as climate or soil microbial community composition, were more important potential direct drivers of instantaneous N cycling rates, then we would expect to find only weak correlations between N cycling rates and soil properties.

2. Materials and methods

2.1. Study sites

Our study utilized 33 existing research sites at 27 study areas located within 8 out of 10 bioregions in California (Hickman, 1993, Fig. 1; Table S1). The

study sites were chosen to represent a wide continuum in soil properties that could elucidate controls on gross N cycling rates using a regression approach. Mean annual precipitation (MAP) for each site over the period of 1980–2015 was obtained from the daily time step, 1-km grid resolution Daymet data set archived and distributed through the Oak Ridge National Laboratory Distributed Active Archive Center (Table S1, Thornton et al., 2016). Soils from the top 10 cm of mineral horizons were collected from 27 sites in January 2007 (wet season), and from six high elevation sites in the Sierra Nevada in May 2007 after snowmelt. A characteristic of Mediterranean climates is dry summers and wet winters, so we timed the soil sampling to avoid the pulses of high microbial activity that occur with the first precipitation events of the wet season (Chou et al., 2008; Xiang et al., 2008). We also timed the soil sampling campaigns to maximize the chances that we would collect the soils under field moist conditions that minimize the impact of water addition associated with isotope labeling (e.g., monthly precipitation totals taper off after February).

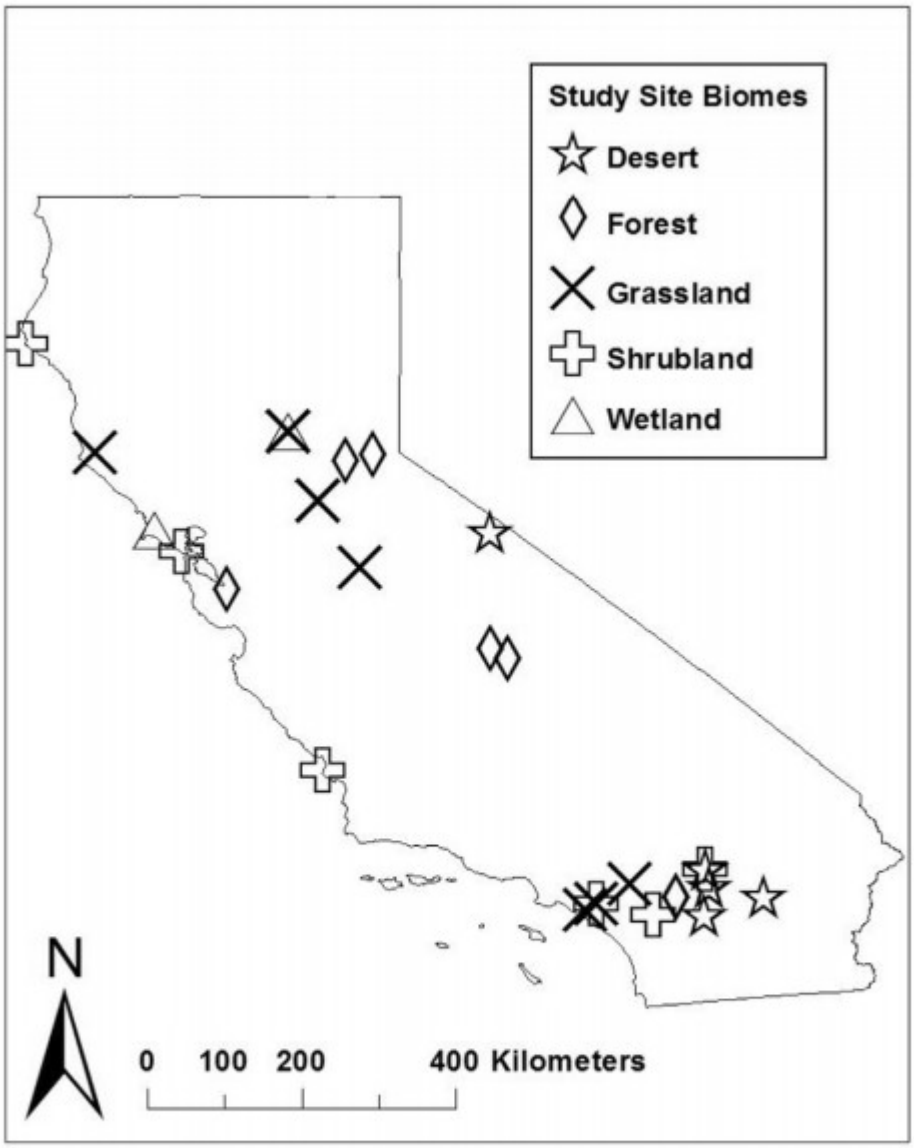

Fig. 1. Locations of the 33 study sites in California, representing five different biomes. Some study sites were co-located, leading to 27 distinct locations represented; global positioning system (GPS) coordinates for each site are listed in Table S1.

We grouped the sites into the following major biomes that represent approximately 97% of the land cover in California: desert, grassland, shrubland, and forest (Lenihan et al., 2003). Alpine and subalpine forests, which were not included in our study, represent the remaining 3% of California. We also included a salt marsh and a spring-fed wetland (Jackson and Allen-Diaz, 2006) to characterize wetlands and broaden the spectrum of ecosystems sampled. Oak woodlands with a grass understory represent 7% of the land area in California (Bolsinger, 1988; Greenwood et al., 1993) and are characterized by faster rates of N cycling under the oak canopies

compared to open grassland areas (Herman et al., 2003; Jackson et al., 1990). Here, the oak woodland soils followed the same patterns as the grassland soils for the suite of soil properties measured (data not shown), so we grouped them with grasslands rather than forests.

The sites included here span a range of background N deposition rates (0.6–18.4 kg N ha^{-1} y^{-1}) and included three sites that received experimental fertilizer additions (Table S1). Background total (wet plus dry) atmospheric N deposition rates for the sites were obtained from the 4-km grid resolution Community Multiscale Air Quality model for California, which was up-to-date at the time that this study was conducted in 2006 (Tonnesen et al., 2007). The grassland soil from the University of California-Irvine Arboretum received a total of 76.4 kg N ha^{-1} as NPK (29:3:4) fertilizer in 2006 (Bijoor et al., 2008). The desert soil from Pinto Basin, Joshua Tree National Park received 60 kg N ha^{-1} y^{-1} as NH_4NO_3 during the period 2002–2009 (Allen et al., 2009), and the shrubland soil from Lake Skinner has received 60 kg N ha^{-1} y^{-1} as NH_4NO_3 since 1994 (Sirulnik et al., 2007). Due to the small number of study sites (n = 3) receiving fertilization application, we did not statistically evaluate the effect of fertilization on gross N cycling other than assessing whether or not they were outliers compared to the other study sites.

2.2. Gross nitrogen cycling assays

We measured DNRA and gross N cycling rates to provide a comprehensive view of N transformations, capturing a more complete assessment of N mineralized and consumed than the net rates typically measured (Davidson et al., 1992). We note that short-term laboratory assays may not reflect long-term field rates of gross N cycling (i.e., months to years), especially because of seasonality in field conditions. Disturbance effects of mixing soils for the laboratory assays may also change soil structure and substrate availability to alter rates of N cycling (Booth et al., 2006; Kaur et al., 2010; Schimel et al., 1989). Our goal here was to compare laboratory rates among soils from different ecosystems while maintaining soil moisture and substrate availability for the various N cycling processes similar to field conditions at the time of soil collection. We used the study sites to obtain a wide range of soil variables to elucidate controls on instantaneous N process rates rather than to estimate characteristic rates for each biome.

One soil core from each study site was collected from the top 10 cm of mineral soil and stored in a gas permeable polyethylene bag at ambient temperature for no more than one week. Soil samples collected from the high elevation sites were assayed in a separate batch from the other samples because they were collected in May rather than January. One day before the gross N cycling assays were performed, each soil core was gently broken up by hand to remove large rocks and roots while maintaining some soil aggregation (i.e., the soil samples were not sieved). A 10 g subsample was used for determination of gravimetric soil moisture. A 5 g subsample was extracted in 2 M KCl for colorimetric determination of ammonium (NH_4^+)

and NO_3^- concentrations (Lachat Quik Chem flow injection analyzer, Lachat Instruments, Milwaukee, WI) so that an appropriate amount of ^{15}N label could be added for gross N cycling assays. Separate 90 g soil subsamples were weighed into two gas permeable bags, for $^{15}NH_4^+$ and $^{15}NO_3^-$ addition to determine gross mineralization and nitrification rates, respectively; a 30 g subsample was used for the determination of initial (t_0) NH_4^+ and NO_3^- concentrations for the gross N cycling assays. The remaining soil was air-dried for determination of pH as well as soil total N and soil organic carbon (SOC) concentration.

To accommodate the range in soil NH_4^+ and NO_3^- concentrations among sites, the soil samples were divided into five and four groups so that the initial ^{15}N enrichment would be approximately 10–20 atom % ^{15}N based on the preliminary measurements of soil concentrations of NH_4^+ and NO_3^-, respectively. One mL of the appropriate ^{15}N label solution was added to each 90 g bag of fresh soil, causing only a small change in soil moisture to minimize wetting effects on microbial activity. The soil was then gently mixed by hand (i.e., not slurried) to distribute the ^{15}N label. The soil was incubated in a sealed 500 mL Mason jar with an ambient air headspace for three hours. The incubated soil was split for 2 M KCl extraction, 0.5 M K_2SO_4 extraction, and fumigation in chloroform for five days before extraction in 0.5 M K_2SO_4. The initial ^{15}N enrichment was determined from the ^{15}N label added and the initial NH_4^+ and NO_3^- pools (Silver et al., 2005; Yang et al., 2015). We assumed that the background ^{15}N enrichment of the NH_4^+ and NO_3^- pools were at natural abundance, 0.3663 atom %. The ^{15}N enrichment of NH_4^+ and NO_3^- were determined using the diffusion technique (Herman et al., 1995) and analysis on an isotope ratio mass spectrometer (PDZ Europa, Limited, Crewe, UK). Gross N mineralization and nitrification rates as well as gross NH_4^+ and NO_3^- consumption rates were calculated according to Kirkham and Bartholomew (1954), and DNRA rates were calculated according to Silver et al. (2005). The ratios of gross production to gross consumption for NH_4^+ and NO_3^- were used to assess whether N cycling rates were substantially impacted by the ^{15}N-labeling process, where significant deviations from 1.0 suggest potential impacts (Stark and Hart, 1997).

2.3. Microbial biomass nitrogen and soil chemical analyses

Microbial biomass N was determined on field-fresh soils. Alkaline potassium persulfate digestion followed by colorimetric determination of NO_3^- was used to determine total N in the K_2SO_4 extracts (Cabrera and Beare, 1993). Microbial biomass N (MBN) was calculated from the difference in total N

between fumigated and unfumigated soils, assuming an extraction efficiency of 0.54 (Brookes et al., 1985).

For the remaining soil chemical analyses, air-dried soil samples were passed through a 2 mm sieve and then ground by hand using a mortar and pestle. Before grinding, roots and large pieces of organic matter were picked out by hand. We tested for the presence of carbonates by adding a drop of 1 M HCl to a subsample of each soil to check for effervescence. If effervescence occurred (which was the case only for the desert soils), then inorganic C was removed from 2 g ground air-dried soil by twice-washing with 30 mL 0.1 N HCl (allowing the soil slurry to stand for 1 h each time), twice-washing with 30 mL DI, and then freeze-drying (unpublished protocol from T. Baisden, Institute of Geological & Nuclear Sciences). After each washing, the soil slurry was centrifuged, and the supernatant was removed via aspiration. The ground soils were analyzed on an elemental analyzer (CE Elantec, Lakewood, New Jersey) for concentrations of soil organic C (SOC) and total N, and the C:N ratio by mass. Soil pH was measured in soil slurries with a 2:1 ratio of DI water to air-dried soil (MacLean, 1982).

2.4. Data analyses

Statistical analyses were performed using SYSTAT Version 13 (SPSS Inc., Evanston, IL). Estimates of negative gross rates were omitted from analyses; this led to fewer than 33 data points for gross N cycling rates. All data, except soil C:N ratios and gross N mineralization rates, were log10-transformed to achieve normal distributions. We used a one sample t-test to determine if the ratios of gross production to gross consumption for NH_4^+ and NO_3^- differed significantly from one for the entire dataset. We also used a one sample *t*-test to determine if DNRA rates for the entire dataset differed significantly from zero. We compared soil properties and gross N cycling rates among biomes using ANOVAs and Fisher's LSD multiple comparison tests, which provided the statistical power needed for the relatively small sample sizes per biome. We considered the sites as replicates within each biome. Because the sample size for wetlands was small (n = 2) and unbalanced with those for the other biomes (n = 7–10), we did not include wetlands in the comparisons among biomes. We used least squares linear regressions to explore relationships among soil properties and gross N cycling rates across all biomes, taking a backwards stepwise approach to determine the best fit model that minimized the corrected Akaike information criterion (AICc) using 0.05 as the critical p-value for retaining explanatory variables in the model. We chose this approach because we wanted to consider all possible explanatory variables that could drive N cycling rates, and the AICc reduces the probability of selecting models with extra parameters. Where AICc values are comparable for multiple models, we present all models. We avoided multicollinearity by not including highly correlated soil variables (e.g., soil organic C and total N) in the same regression models. Background atmospheric N deposition rates and MAP

were also considered as potential explanatory variables in the regression models. We identified statistical outliers using the Hadi robust outlier detection test and present data analyses with and without the one outlier identified based on a low gross nitrification rate (i.e. an annual grassland soil from the Irvine Ranch Land Reserve). Statistical significance was determined at $P < 0.05$.

3. Results

3.1. Soil properties across biomes

Most soil properties varied significantly and predictably across biomes (Figs. 2 and 3). Desert soils were distinct from soils from all other biomes with respect to many soil properties, including lower soil moisture (Fig. 2a), SOC (Fig. 2c), total N (Fig. 3a), and MBN (Fig. 3b), as well as higher pH (Fig. 2b; $P < 0.001$ for all). Mean annual precipitation in the desert sites was also different from all other study sites ($F_{4,28} = 6.59$, $P = 0.001$), with an average of 250 ± 53 (±SE) mm for the desert sites compared to 780 ± 85 mm for all other sites. Forest soils had the highest SOC (Fig. 3c) and soil C:N ratios (Fig. 2d), as well as the lowest soil NO_3^- concentrations (Fig. 3c) ($P < 0.001$ for all). Although wetlands could not be included in the statistical analyses due to small sample size ($n = 2$), they clearly had the highest soil moisture (Fig. 2a) and MBN (Fig. 3b) of all biomes. Wetlands also had the lowest NO_3^- concentrations, which were undetectable with an analytical detection limit of 0.01 mg N kg^{-1} (Fig. 3c).

Total N concentrations were strongly correlated to many soil variables. The strongest relationship was with SOC concentrations (Fig. 4a), which explained 88% of the variability in total N ($N = 33$, $P < 0.001$). The strong correlation between total N and SOC resulted in similar relationships for both C and N with other soil properties. Total N was positively correlated with MAP ($R^2 = 0.50$, $N = 33$, $P < 0.001$). Total N concentrations were negatively correlated to pH across all biomes ($R^2 = 0.32$, $N = 33$, $P = 0.001$, Fig. 3c). This relationship may have reflected collinearity between pH and MAP, which were negatively correlated ($R^2 = 0.50$, $N = 33$, $P < 0.001$). Microbial biomass N exhibited a strong positive relationship with total N concentrations ($R^2 = 0.65$, $N = 33$, $P < 0.001$, Fig. 4d). Mean annual precipitation was also positively correlated to MBN ($R^2 = 0.40$, $N = 33$, $p = 0.001$). pH was the weakest predictor of MBN, explaining 23% of its variability ($N = 33$, $P < 0.001$).

3.2. Patterns in gross nitrogen cycling rates across biomes

Gross rates of N transformations varied significantly among biomes despite high variability within biomes. Gross N mineralization rates were marginally higher in grasslands compared to deserts and forests, and also marginally higher in shrublands compared to deserts ($F_{3,23} = 2.49$, $P = 0.09$, Fig. 5a). Across biomes, gross N mineralization rates ranged from 2.36 to 81.4 mg N

kg^{-1} d^{-1}, with the highest rate from a spring-fed wetland soil and the lowest rate from the botanical garden soil (classified as a grassland). Forest soils exhibited lower gross nitrification rates than soils from all other biomes ($F_{3,18}$ = 4.09, P = 0.02, Fig. 5a). Gross nitrification rates were greatest in a chaparral shrubland soil from the Irvine Ranch Land Reserve (71.1 mg N kg^{-1} d^{-1}) and lowest in a mixed conifer forest soil from the Blodgett Forest Research Station (0.26 mg N kg^{-1} d^{-1}).

Dissimilatory NO_3^- reduction to NH_4^+ was detectable in soil samples from all biomes, with rates significantly different from zero across all samples (N = 25, P = 0.007). Rates of DNRA were highly variable, ranging from 0.01 mg N kg^{-1} d^{-1} in a desert soil to 4.9 mg N kg^{-1} d^{-1} in a grassland soil. Rates of DNRA did not differ significantly among biomes ($F_{3,20}$ = 1.19, P = 0.34, Fig. 5c).

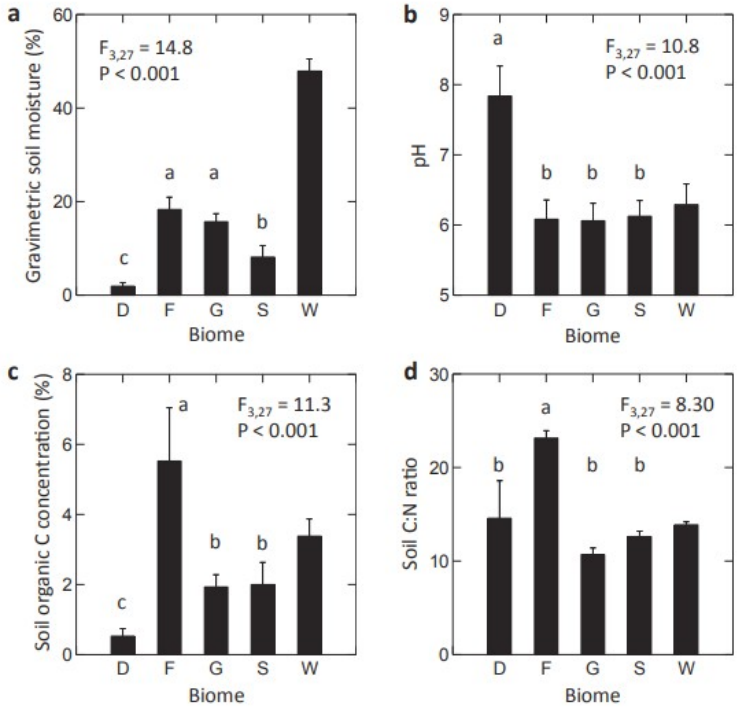

Fig. 2. (a) Gravimetric soil moisture, (b) pH, (c) soil organic C concentration, and (d) soil C:N ratio by biome, where D = desert (n = 7), F = forest (n = 7), G = grassland (n = 10), S = shrubland (n = 7), and W = wetland (n = 2). Bars represent means and each error bar represents one standard error using sites within biomes as replicates. Letters indicate statistically significant differences among biomes determined using ANOVA and Fisher's LSD mean separations test; wetlands were excluded from these analyses due to small sample size.

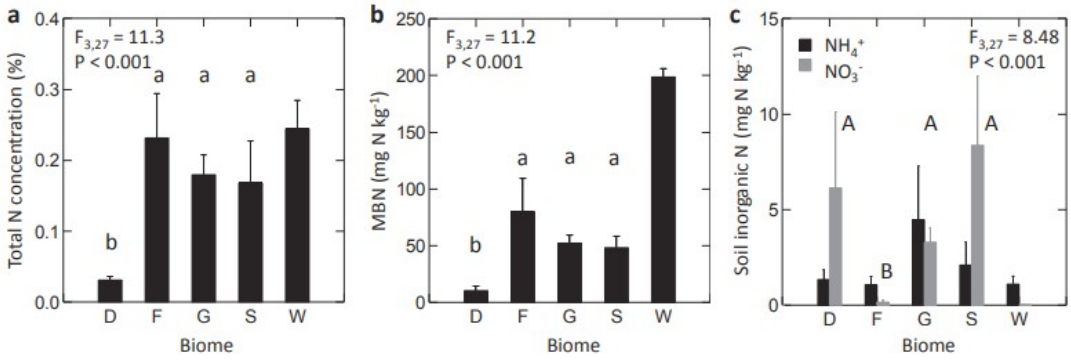

Fig. 3. (a) Total N concentrations, (b) microbial biomass nitrogen (MBN), and (c) soil ammonium (NH_4^+, black bars) and nitrate (NO_3^-, gray bars) concentrations by biome, where D = desert, F = forest, G = grassland, S = shrubland, and W = wetland. Bars represent means and each error bar represents one standard error using sites within biomes as replicates. Significant differences among biomes were determined by ANOVA and Fisher's LSD means separation test, and are indicated by different lowercase letters for variables shown in black bars and by different uppercase letters for variables shown in gray bars; wetlands were excluded from ANOVAs due to small sample size (n = 2).

Gross consumption rates of NH_4^+ and NO_3^- averaged 40.1 ± 6.9 mg N kg^{-1} d^{-1} and 5.8 ± 2.5 mg N kg^{-1} d^{-1}, respectively. Neither gross NH_4^+ consumption rates nor gross NO_3^- consumption rates differed among biomes (Fig. 5b). The ratio of gross NH_4^+ production to consumption did not differ significantly from 1 (N = 27, P = 0.17), averaging 1.0 ± 0.15 across all samples; the ratio did not differ among biomes (Fig. S1). The ratio of gross NO_3^- production to consumption was significantly greater than 1 (N = 19, P = 0.001), averaging 23 ± 15. The ratios for NO_3^- could not be compared among biomes due to small sample sizes caused by the omission of five samples with negative gross NO_3^- consumption rates (Fig. S1).

3.3. Controls on gross nitrogen cycling rates

Gross N mineralization rates were correlated to many soil variables. Rates were most strongly correlated to soil moisture as a single variable (R^2 = 0.30, N = 29, P = 0.002, Fig. 6a). Gross N mineralization was also correlated to MBN (R^2 = 0.23, N = 29, P < 0.001, Fig. 6b) and total N concentration (R^2 = 0.16, N = 29, P = 0.03, Fig. 6c). Although neither SOC concentration nor soil C:N ratios alone were correlated with gross N mineralization, together they explained 27% of the variability in gross N mineralization (N = 29, P = 0.02). Soil moisture and soil C:N ratios together explained almost half of the variability in gross N mineralization rates across biomes (R^2 = 0.46, N = 29, P < 0.001, Table 1).

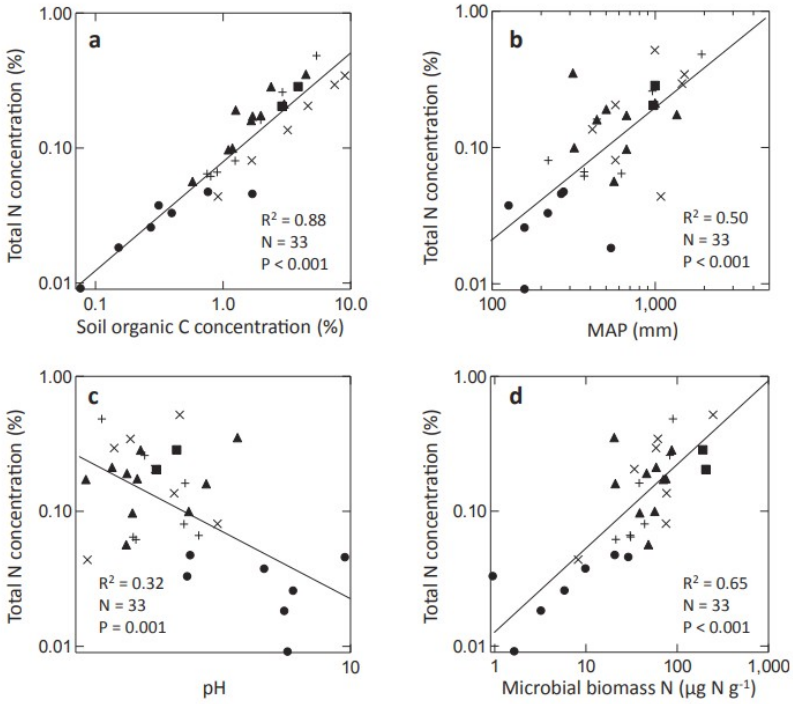

Fig. 4. Total N concentration versus (a) soil organic C concentration with the line representing the regression equation, log(y) = [0.81 * log(x)]−1.10, (b) mean annual precipitation with a dashed regression line for deserts, log(y) = [0.98 * log(x)]−3.65, (c) pH with the regression line, log(y) = [-3.46 * log(x)] + 1.84, and (d) microbial biomass N (MBN) with a regression line, log(y) = [0.63* log(x)]−1.92. Symbols represent ecosystem types: circles indicate deserts, crosses indicate forests, triangles indicate grasslands, pluses indicate shrublands, and squares indicate wetlands. All axes are on $\log_{10}$ scales.

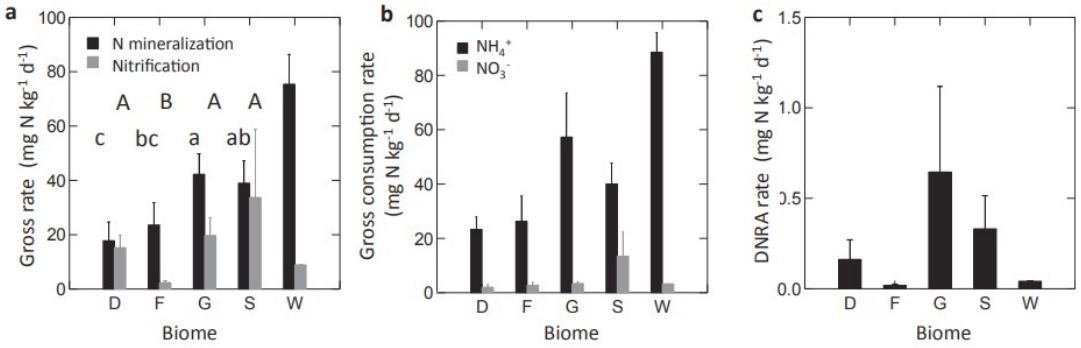

Fig. 5. (a) Gross N mineralization rates (black bars) and gross nitrification rates (gray bars), (b) gross NH_4^+ consumption rates (black bars) and gross NO_3^- consumption rates (gray bars), and (b) dissimilatory nitrate reduction to ammonium (DNRA) rates by biome, where D = desert, F = forest, G = grassland, S = shrubland, and W = wetland. Bars represent means and each error bar represents one standard error using sites within biomes as replicates. Significant differences among biomes are indicated by different lowercase letters for variables shown in black bars and different uppercase letters for variables shown in gray bars. Biome was a marginally significant factor for gross N mineralization rates ($F_{3,23} = 2.49$, $P = 0.09$) and a significant factor for gross nitrification rates ($F_{3,18} = 4.09$, $P = 0.02$); wetlands were excluded from these ANOVAs due to small sample size (n = 2 for gross N mineralization and n = 1 for gross nitrification and DNRA).

Gross nitrification rates were positively correlated to soil NO_3^- concentrations (Fig. 7a, $R^2 = 0.34$, N = 23, p = 0.003) and negatively correlated to soil C:N ratios ($R^2 = 0.31$, N = 23, P = 0.005, Fig. 7b). An annual grassland soil from the Irvine Ranch Land Reserve exhibiting the second lowest gross nitrification rate out of all soil samples was identified as an outlier in both of these regression models, which best predicted gross nitrification rates based on AICc values.

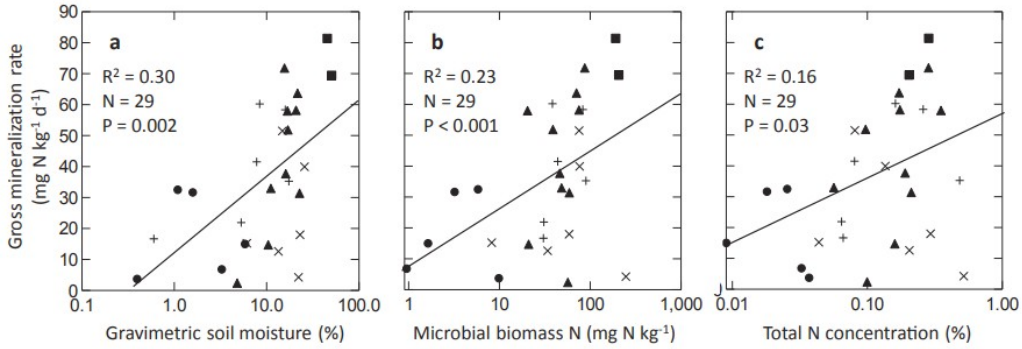

Fig. 6. Gross N mineralization rates versus (a) gravimetric soil moisture with the regression line, y = [24.4 * log(x)] + 12.2, and AICc = 259 (b) microbial biomass N with the regression line, y = [18.8 * log(x)] + 7.10, and AICc = 262, and (c) total N concentration with the regression line, y = [20.8 * log(x)] + 55.5, and AICc = 265. The solid lines represent regression lines. Symbols representing ecosystem types are as in Fig. 4. All x-axes are on $\log_{10}$ scales.

Table 1
Regression equations that best predicted soil nitrogen pools and fluxes.[a]

Dependent variable	Independent variable	Regression coefficient	P-value	n[b]	R^2	P-value	AICc
Total N concentration	Constant	−1.10 ± 0.027	<0.001	33	0.88	<0.001	−27.4
	SOC concentration	0.81 ± 0.053	<0.001				
Soil NH_4^+ concentration	Constant	0.69 ± 0.088	<0.001	25	0.75	<0.001	4.88
	Dissimilatory NO_3^- reduction to NH_4^+ (DNRA) rate	0.59 ± 0.070	<0.001				
Soil NO_3^- concentration	Constant	1.01 ± 0.29	0.002	25	0.41	0.001	65.8
	DNRA rate	0.92 ± 0.23	0.001				
Gross N mineralization rate	Constant	31.6 ± 10.0	0.004	29	0.46	<0.001	255
	Gravimetric soil moisture	30.1 ± 6.74	<0.001				
	Soil C:N ratio	−1.84 ± 0.68	0.01				
Gross nitrification rate	Constant	1.00 ± 0.11	<0.001	23[c]	0.34	0.003	39.0
	Soil NO_3^- concentration	0.34 ± 0.10	0.003				
Gross nitrification rate	Constant	1.77 ± 0.30	<0.001	23[c]	0.31	0.005	39.9
	Soil C:N ratio	−0.064 ± 0.021	0.005				
DNRA rate	Constant	−1.16 ± 0.053	<0.001	25	0.89	<0.001	12.3
	Soil NH_4^+ concentration	1.01 ± 0.12	<0.001				
	Soil NO_3^- concentration	0.28 ± 0.059	<0.001				
	SOC concentration	0.33 ± 0.12	0.01				

[a] All variables were $\log_{10}$-transformed except for soil C:N ratios and gross N mineralization rates.
[b] All samples were pooled for these analysis. Though there were 33 soil samples overall, the sample size differs among regression models due to estimates of negative gross rates that were omitted from analyses.
[c] Site 24 included in the regression analysis was identified as an outlier.

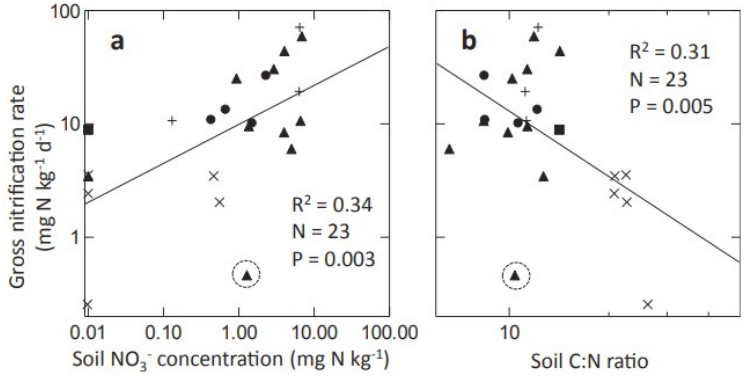

Fig. 7. Gross nitrification rates versus (a) soil NO_3^- concentrations and (b) soil C:N ratios. The solid lines represent the regression lines for data sets including the circled outlier (Site 24, grassland) identified in both regression models; regression coefficients are reported in Table 1. Regression statistics with the outlier excluded are as follows for panels a and b: (a) $R^2 = 0.48$, N = 22, P < 0.001, and (b) $R^2 = 0.48$, N = 22, P < 0.001. Symbols represent ecosystem types: circles indicate deserts, crosses indicate forests, triangles indicate grasslands, pluses indicate shrublands, and squares indicate wetlands. All axes are on $\log_{10}$ scales.

Nitrate concentrations alone explained 41% of the variability in DNRA rates (N = 25, P < 0.001, Fig. 8a), and this explanatory power increased to 61% when only considering soils with detectable NO_3^- concentrations (N = 21, P <

0.001, Fig. 8a). Soil NH_4^+ concentrations were also positively correlated to DNRA rates ($R^2 = 0.75$, N = 25, $P < 0.001$ Fig. 8b). Soil NH_4^+ and NO_3^- concentrations together with gross nitrification rates best predicted DNRA rates with $R^2 = 0.89$ (N = 25, $P < 0.001$, Table 1).

Soil NH_4^+ concentrations were well predicted by the combination of gross nitrification and DNRA rates, which had negative and positive correlations with soil NH_4^+, respectively ($R^2 = 0.80$, N = 20, $P < 0.001$, Table 1). Gross N mineralization was also correlated to soil NH_4^+ ($R^2 = 0.16$, N = 29, $P = 0.03$). Soil NO_3^- concentrations were best predicted by DNRA rates ($R^2 = 0.41$, N = 25, Table 1).

Atmospheric N deposition rates were not correlated with any soil properties or gross N cycling rates despite a wide range in rates of deposition (0.6–18.4 kg N ha^{-1} y^{-1}), although rates were relatively low compared to the highest deposition rates in the Northeast U.S. (>40 kg N ha y^{-1}) or commercial and experimental fertilizer application rates (100–400 kg N ha y^{-1}) that are known to alter N cycling rates (Aber et al., 1989). Only 4 sites located in the urban areas of Irvine and Riverside, California received greater than 10 kg N ha^{-1} y^{-1}. Atmospheric N deposition rates did not differ significantly among biomes but trended lower in deserts compared to all other biomes ($F_{3,27} = 2.52$, $P = 0.08$). Soils from sites that received experimental fertilization did not appear as outliers in any of the analyses.

4. Discussion

4.1. Biome level differences in soil properties and gross nitrogen cycling rates

We found remarkably predictable patterns in soil properties and gross N cycling rates across biomes despite high variability within biomes. We expected high intra-biome variability for the desert and shrubland biomes because soil samples from these biomes were collected from either interspaces or beneath plants, as typically sampled by long-term investigators at each research site. Plants act as “islands of fertility” in deserts so that soil N content, inorganic N concentrations, and N cycling rates are often elevated beneath plants relative to interspaces (Billings et al., 2004; Schade and Hobbie, 2005; Schlesinger and Pilmanis, 1998). This effect has also been observed beneath tree canopies in oak woodlands (Herman et al., 2003; Jackson et al., 1990), which we classified as grasslands, but only one of six oak woodland sites were sampled from beneath a tree canopy. Despite this known source of intrabiome variability, the variance in soil properties and N cycling rates was comparable across all biomes, suggesting that sampling location differences were less important than the cross-biome differences. While one sampling time point served our purposes for elucidating controls on N cycling rates, given the strong seasonality at the

study sites, we cannot use the biome means from this one time point as estimates of characteristic rates for each biome. Our results, nonetheless, indicate that distinct patterns exist in instantaneous N pools and fluxes at the scale of biomes in California.

Desert soils exhibited similar short-term gross N cycling rates to the other biomes despite their distinct soil properties that could have limited soil microbial activity. They had low soil moisture, low SOC and total N concentrations, low MBN, and high pH compared to other biomes as expected (Gallardo and Schlesinger, 1992; Wang et al., 2014). This could be due to the significantly lower MAP in the desert sites compared to all other biomes (Jenny and Leonard, 1934; Post et al., 1985). It is unlikely that N cycling was stimulated by the addition of ^{15}N label in deionized water (Willison et al., 1998) because we increased soil moisture by only 1–2%. This methodological artifact is a greater concern when using intact soil cores because a larger volume of solution is required to distribute the ^{15}N label throughout the soil (Davidson et al., 1991; Sparling et al., 1995). Sites with inherently low soil moisture (<6%), which included deserts as well as some grasslands and shrublands, followed the general relationships between N cycling rates and soil properties. This suggests that the addition of ^{15}N label in a small volume of water relative to the mass of soil assayed did not stimulate microbial N cycling. Instead, N cycling in the desert soils may have been sustained by the activity of fungi, which are more drought tolerant than bacteria (Adebayo and Harris, 1971; Wilson and Griffin, 1975) and can be more abundant than bacteria in desert soils (Clark et al., 2009).

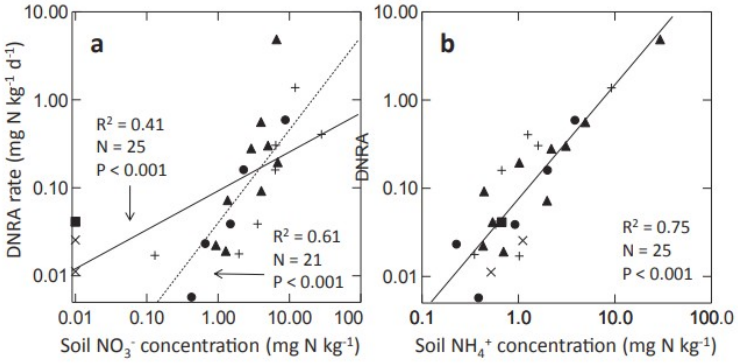

Fig. 8. Dissimilatory NO_3^- reduction to NH_4^+ (DNRA) rates versus (a) soil NO_3^- concentrations with the regression line for all data, log(y) = [1.08 * log(x)]−1.42, and (b) soil NH_4^+ concentrations with the regression line, log(y) = [1.25 * log(x)]−1.10. The solid lines represent the regression lines including all data points; the dashed line represents a regression line excluding four soil samples with negligible standing NO_3^- pools (from Sites 13, 14, 22, and 32 representing two forest sites, one grassland, and one wetland). Symbols represent ecosystem types: circles indicate deserts, crosses indicate forests, triangles indicate grasslands, pluses indicate shrublands, and squares indicate wetlands. All axes are on $\log_{10}$ scales.

4.2. Patterns in and controls on mineralization

Gross N mineralization rates were best predicted by soil moisture and soil C:N ratios, which exhibited positive and negative relationships, respectively. These results suggest that the low gross N mineralization rates of the desert soils were associated with their low soil moisture rather than their low MBN or total N, both of which were only weakly correlated to gross N

mineralization. Surprisingly, gross nitrification and DNRA were comparable in the desert soils to those in the grasslands and shrublands, suggesting that NO_3^- processing was less sensitive to soil moisture than mineralization. Gross N mineralization rates were marginally lower in forests compared to grasslands, likely due to the high C:N ratios of forest soil organic matter that yield less N per unit of mineralized soil organic matter (Hart et al., 1994). Although deserts and shrublands had similarly low soil C:N ratios compared to the forests, gross N mineralization rates in those soils were not significantly higher than in the forest soils. This may be due to the lower soil moisture in deserts and shrublands compared to the forests and grasslands limiting mineralization in those soils. This suggests that soil moisture was the proximate control on N mineralization whereas soil C:N ratios played a secondary role.

4.3. Patterns in and controls on nitrification

Overall, the only strong predictor of gross nitrification rates was soil C:N ratios. The negative relationship between gross nitrification and soil C:N was driven by the forest soils, which had soil C:N ratios greater than 20. However, not all forests have such high soil C:N ratios. Our forest sites were dominated by coniferous trees, which have higher litter C:N ratios than deciduous trees (Augusto et al., 2002; Booth et al., 2005; McGroddy et al., 2004). Thus, deciduous forests with lower soil C:N ratios may have higher gross nitrification rates comparable to the other biomes in our study. Cross-site comparisons of forests that included both deciduous and coniferous trees have also documented negative relationships between soil C:N ratios and both gross nitrification (Bengtsson et al., 2003; Christenson et al., 2009) and net nitrification (Lovett et al., 2004; Venterea et al., 2003). Christenson et al. (2009) found lower gross nitrification rates in forests with lower gross mineralization rates and hypothesized that NH_4^+ supply likely limited nitrification in mineral soil horizons. In support of this hypothesis, the meta-analysis by Booth et al. (2005) showed that gross N mineralization was the strongest predictor of gross nitrification (with $R^2 = 0.32$) across woody, grassland, and agricultural ecosystems. In contrast, we did not find a correlation between gross N mineralization and nitrification. Deserts, which had the lowest gross N mineralization rates, exhibited similar nitrification rates to the shrublands and grasslands. Although gross N mineralization rates were marginally lower in forests compared to grasslands, only 15% of NH_4^+ produced was nitrified in the forests compared to 47–86% in the other biomes. This suggests that NH_4^+ production rates did not limit nitrifiers in the forests, but rather, that another factor limited nitrifier activity. At the high soil C:N ratios found in our forest sites, heterotrophs may have outcompeted autotrophic nitrifiers for NH_4^+ (Riha et al., 1986; Verhagen and Laanbroek, 1991), thereby limiting nitrification rates. Soil C:N ratio was the strongest predictor of gross nitrification rates across all biomes, but other factors not

included in our study, such as nitrifier abundance (Hawkes et al., 2005; Petersen et al., 2012; Ribbons et al., 2016), were likely important as well because soil C:N ratios explained only a third of the variability in gross nitrification rates.

4.4. Patterns in and controls on DNRA

The prevailing conceptual model of DNRA suggests that it is restricted to highly reducing conditions (Buresh and Patrick, 1978) or soils with very high C:N ratios (Tiedje, 1988), yet we observed its occurrence in soils from all biomes. Comparable DNRA rates have been reported for other non-flooded grassland and forest soils (Chen et al., 2015; Rutting et al., 2008; Silver et al., 2001, 2005). Our observations of DNRA in desert soils suggest that it occurred in the presence of O_2 rather than simply in anaerobic microsites within soil aggregates (Sexstone et al., 1985) or in microsites of high biological O_2 consumption that exceed diffusive resupply of O_2 (Parkin, 1987). Morley and Baggs (2010) also observed DNRA in well-mixed oxygenated soil slurries that likely did not harbor anaerobic microsites. Higher DNRA rates under aerobic compared to anaerobic soil conditions have even been reported (Yang et al., 2015), possibly due to greater O_2 tolerance of DNRA organisms than denitrifiers, which compete with DNRA for NO_3^- (Fazzolari et al., 1998; Pett-Ridge et al., 2006). Our data showed a strong positive correlation between DNRA rates and soil NO_3^- concentrations in support of previous studies suggesting that DNRA is limited by NO_3^- (Silver et al., 2001; Pett-Ridge et al., 2006). Rates of DNRA were not correlated with gross nitrification rates because NO_3^- availability for DNRA could be influenced not only by gross NO_3^- production via nitrification (Zhang et al., 2015) but also by competition for NO_3^- via denitrification (Yang et al., 2015) or by microbial NO_3^- immobilization (Davidson et al., 1992; Hart et al., 1994; Stark and Hart, 1997).

The widespread occurrence of DNRA suggests that it may play a more important role in terrestrial N cycling than previously thought. Gross nitrification, a process which consumes NH_4^+, exerted a negative control on soil NH_4^+ concentrations; in contrast, DNRA, a process which produces NH_4^+, exerted a positive control. These two variables together explained 80% of the variability in soil NH_4^+ concentrations, suggesting that the balance between gross nitrification and DNRA rates can be predictive of soil NH_4^+ at the biome scale. Heterotrophic immobilization of NH_4^+ could be another important predictor of soil NH_4^+ concentrations that could explain the remaining 20% of the variability in soil NH_4^+.

4.5. Methodological considerations

The experimental design used for this study was intended to elucidate the relationships among soil properties and instantaneous gross N cycling rates; thus, the rates reported here may not be characteristic of in situ rates for each biome for several reasons. First, N cycling processes are highly dynamic and responsive to seasonal changes in temperature and precipitation (Austin et al., 2004; Parker and Schimel, 2011). Therefore, multiple time points from a given ecosystem would be needed to better estimate the magnitude of the N fluxes over an annual time scale that integrates over the seasonal changes. Second, the laboratory incubations were conducted at a single constant temperature across all soils to remove temperature as a driving factor in the observed N cycling rates. However, this temperature regime does not reflect in situ patterns. Third, we used gently mixed (i.e., not sieved) soil for the assays to allow us to relate multiple N cycling processes and soil properties to the same homogenous soil sample, facilitating our objective to correlate these variables with each other. Soil mixing can alter gross rates of N mineralization and nitrification (Booth et al., 2006; Kaur et al., 2010; Schimel et al., 1989). It is thought that mixing breaks up soil aggregates to release physically protected organic matter, thereby increasing substrate availability for mineralization to stimulate gross N mineralization rates (Booth et al., 2006; Schimel et al., 1989). The gross N mineralization rates we observed were within the range of values reported in the Booth et al. (2005) meta-analysis, which found no significant difference in rates documented in studies using intact versus mixed soils. This suggests that using mixed soils does not consistently bias measured gross N mineralization rates higher or lower than rates measured in intact soils. The mixing of soil also homogenizes the distribution of organic matter and could potentially inhibit nitrification by favoring heterotrophs that compete better for NH_4^+ in C-rich environments (Booth et al., 2006). However, there is no evidence of this effect (Booth et al., 2006; Kaur et al., 2010). Rather, increased net nitrification rates in mixed soils are driven by the suppression of microbial NO_3^- assimilation by well-distributed NH_4^+ (Booth et al., 2006; Kaur et al., 2010; Schimel et al., 1989). Intact soil cores may preserve soil structure and native substrate availability, but they do not necessarily yield more accurate estimates of gross N cycling rates because they are vulnerable to artifacts associated with biases in isotope label distribution (Davidson et al., 1991).

Comparisons of gross production rates to gross consumption rates can be useful for determining if soil mixing or other aspects of the ^{15}N-labeling procedure affected N cycling in the soils (Stark and Hart, 1997). We found that the ratio of NH_4^+ production to consumption was not significantly from 1, suggesting that the processes producing and consuming NH_4^+ were generally not affected by the experimental procedures. We expected that $^{15}NO_3^-$-

addition could stimulate NO_3^- consumption, leading to a ratio of NO_3^- production to consumption less than 1 (Davidson et al., 1991, 1992; Stark and Hart, 1997). However, this ratio was greater than 1, suggesting that the experimental procedures may have instead stimulated nitrification relative to the processes consuming NO_3^- or inhibited the NO_3^--consuming processes. Given that soil mixing is likely to inhibit nitrification (as mentioned above) and the ratio of NH_4^+ production to consumption suggests that these processes remained in balance, the latter explanation is more likely. As mentioned above, soil mixing can distribute NH_4^+ to cause the suppression of microbial NO_3^- assimilation, a potentially important fate of NO_3^- that was not measured in this study (Davidson et al., 1992; Stark and Hart, 1997). Though changes in rates of microbial NO_3^- assimilation could cascade through the soil N cycle, our evidence suggests that the N transformations considered in this study were not directly impacted by the experimental procedures.

5. Conclusions

Despite differences in vegetation type, atmospheric N deposition rates, and local climate, among other factors, ecosystems across the diverse bioregions in this Mediterranean climate zone grouped into biomes that exhibited predictable patterns in soil properties and instantaneous N cycling rates. Deserts were distinct from all other biomes in terms of most soil properties evaluated, presumably due to low MAP, but the relationships between desert soil properties and N cycling rates were consistent with those for the other biomes. This consistency across all biomes adds to the growing body of evidence that suggests that the fundamental controls on biogeochemical cycling are broadly applicable across bioclimatic, soil, and vegetation classifications (Cleveland and Liptzin, 2007; Fierer and Jackson, 2006; Fierer et al., 2009; Jones et al., 2009; Manzoni et al., 2008; Parton et al., 2007).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.01.004.

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