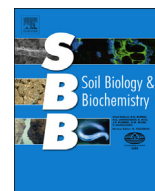




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Short communication

Do we need to understand microbial communities to predict ecosystem function? A comparison of statistical models of nitrogen cycling processes

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ABSTRACT

Despite the central role of microorganisms in biogeochemistry, process models rarely explicitly account for variation in communities. Here, we use statistical models to address a fundamental question in ecosystem ecology: do we need to better understand microbial communities to accurately predict ecosystem function? Nitrogen (N) cycle process rates and associated gene abundances were measured in tropical rainforest soil samples collected in May (early wet season) and October (late wet season). We used stepwise linear regressions to examine the explanatory power of edaphic factors and functional gene relative abundances alone and in combination for N-cycle processes, using both our full dataset and seasonal subsets of the data. In our full dataset, no models using gene abundance data explained more variation in process rates than models based on edaphic factors alone, and models that contained both edaphic factors and community data did not explain significantly more variation in process rates than edaphic factor models. However, when seasonal datasets were examined separately, microbial predictors enhanced the explanatory power of edaphic predictors on dissimilatory nitrate reduction to ammonium and N₂O efflux rates during October. Because there was little variation in the explanatory power of microbial predictors alone between datasets, our results suggest that environmental factors we did not measure may be more important in structuring communities and regulating processes in October than in May. Thus, temporal dynamics are key to understanding the relationships between edaphic factors, microbial communities and ecosystem function in this system. The simple statistical method presented here can accommodate a variety of data types and should help prioritize what forms of data may be most useful in ecosystem model development.

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Information on microbial communities is rarely explicitly considered in large-scale ecosystem models. Instead, most such models implicitly assume that microbial activity can be represented by mathematical equations that apply across diverse environments

(Todd-Brown et al., 2012). However, recent work supports predictive relationships between microbial traits and ecosystem function (Follows et al., 2007; Allison, 2012). Thus, a fundamental question for ecosystem ecology remains widely debated: When do we need to understand details about microbial communities to accurately predict process (e.g., Carney and Matson, 2005; van der Heijden et al., 2008; Leff et al., 2012; Petersen et al., 2012)?

In particular, the *added* value of data on microbial traits – or the predictive power of data on microbial community traits above and beyond that of environmental factors alone – has not yet been

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Table 1
Multiple linear regressions were constructed with three sets of predictors for each process. (1) edaphic variables, (2) relative gene abundances, and (3) both edaphic variables and relative gene abundances. Predictors and statistical results of best-fit models are presented in Table 1. Edaphic models versus overall models were compared using ANOVA, and the results are also presented above.

Process		Edaphic model	Relative gene abundance model	Overall model	Edaphic – overall model comparison
Nitrification	Predictors	NH ₄ _pool, NH ₄ _pool*pH, pH	amoA	amoA, NH ₄ _pool, pH*amoA, pH	$F(19,18) = 3.37$ $p = 0.08$
	Statistical Results	Model $p = 0.007$ Adj. $R^2 = 0.38$	Model $p = 0.06$ Adj. $R^2 = 0.12$	Model $p = 0.005$ Adj. $R^2 = 0.45$	
DNRA	Predictors	ln(soil_moist), pH, NO ₃ _pool, ln(soil_moist)*pH	napA, narG	ln(soil_moist), NO ₃ _pool, NO ₃ _pool*pH, pH, narG, pH*ln(soil_moist)	$F(20,18) = 3.29$ $p = 0.06$
	Statistical Results	Model $p = 0.001$ Adj. $R^2 = 0.49$	Model $p = 0.002$ Adj. $R^2 = 0.39$	Model $p = 0.0008$ Adj. $R^2 = 0.59$	
¹⁵ N ₂ O Efflux	Predictors	NO ₃ _pool, pH, ln(soil_moist)	nirS*nosZ, nirS, nosZ, nirK_rel	pH, nirS, NO ₃ _pool*nirK, NO ₃ _pool, nirK, ln(soil_moist)*nosZ, ln(soil_moist), nosZ	$F(19,14) = 2.08$ $p = 0.13$
	Statistical Results	Model $p = 0.0008$ Adj. $R^2 = 0.51$	Model $p = 0.0008$ Adj. $R^2 = 0.55$	Model $p = 0.003$ Adj. $R^2 = 0.62$	

explicitly considered. Schimel (2001) noted that many process-based models implicitly consider microorganisms by accounting for variation in factors that regulate microbial community composition, such as pH (Fierer et al., 2007), moisture (Nemergut et al., 2010), substrate availability (Legg et al., 2012), temperature (Shade et al., 2012) and salinity (Lozupone et al., 2007). Yet, communities are not entirely determined by abiotic variables, as factors including dormancy (Jones and Lennon, 2010; Lennon and Jones, 2011), priority effects (Fukami, 2004), and neutral community assembly processes (Ferrenberg et al., 2013; Nemergut et al., 2013) can also structure communities. The degree to which such factors affect the composition, functional traits, and activity of a given microbial community will affect the value of microbial data in predicting ecosystem processes beyond that of environmental factors alone.

Here, we used statistical models to compare the power of edaphic factors to predict soil microbial processes with and without data on microbial traits. Because data on microbial traits can provide a more accurate representation of functional potential than data on overall community structure (Polz et al., 2006; Burke et al., 2011), we used quantitative polymerase chain reaction (qPCR) data on functional genes for this analysis. We focused on genes involved in nitrogen (N) cycling as well as measurements of nitrification, dissimilatory nitrate reduction to ammonium (DNRA), and nitrous oxide (N₂O) emission rates determined using ¹⁵-N tracers. All data were generated from soils collected in May (early wet season) and October (late wet season) from a lowland tropical forest on the Osa Peninsula, Costa Rica (8°43' N, 83°37' W; Wieder et al., 2013). Abundances of genes involved in nitrification (bacterial and *Thaumarchaeota amoA*), nitrate reduction (*narG* and *napA*), nitrogen

fixation (*nifH*), and denitrification (a likely source of N₂O emissions; *nirS*, *nirK*, and *nosZ*) were used as proxies of microbial trait abundances, as described by Wieder et al. (2013). Edaphic factors, including pH, moisture, NO₃⁻ and NH₄⁺ pools, and total C and N content were collected to describe environmental conditions (Wieder et al., 2013). Because only a subset of the data for which we had qPCR data were used, some of the relationships identified here vary slightly from those presented in Wieder et al. (2013).

Three sets of multiple linear regressions were fit to the data to explain rates of each N-cycle process: (1) models with edaphic predictors only; (2) models with gene abundance predictors (*narG*, *napA*, *nifH*, *nirS*, *nirK*, and *nosZ* relative to bacterial + *Thaumarchaeota* 16S rRNA gene abundance) only; and (3) models with both edaphic and gene relative abundance predictors. Comparisons between edaphic and overall models were conducted using a partial ANOVA to compare the sum of squared errors for each model, and to determine if models with different predictors were significantly different ($\alpha = 0.05$). Finally, we used linear regression to compare the residuals of the best-fit edaphic models and individual gene relative abundance predictors to determine if microbial predictors explained a different proportion of the variance in process than edaphic factors alone. We performed analyses on samples collected during May and October separately as well as on the entire dataset together to examine the effect of temporal dynamics on the relationships between edaphic factors, microbial communities and N-cycling processes.

When examining our data across both seasons combined, we found that edaphic factors yielded more explanatory power than microbial predictors for nitrification (Adj. R^2 of 0.38 vs. 0.12), but

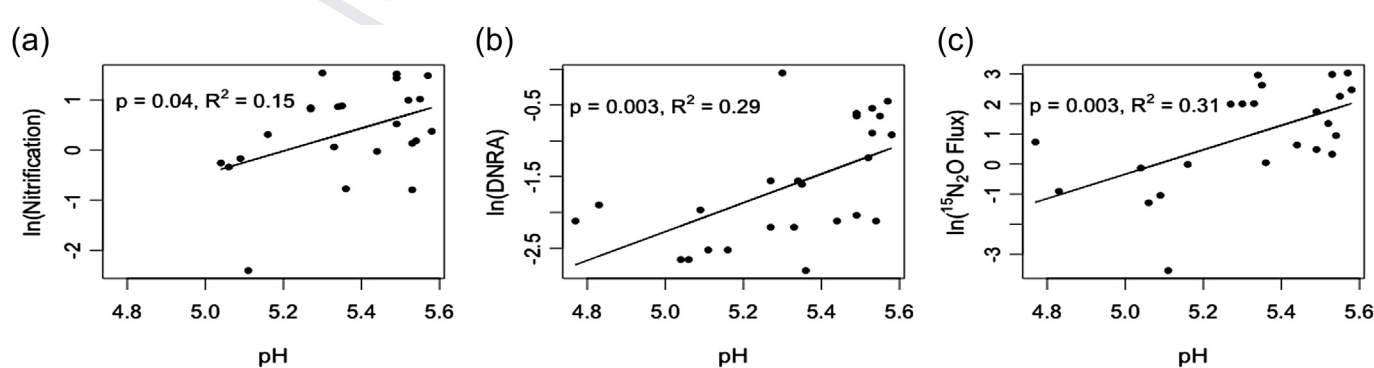


Fig. 1. Univariate models were constructed to evaluate the effect of pH alone on (a) nitrification, (b) DNRA, and (c) ¹⁵N₂O efflux rates. pH was the strongest individual edaphic predictor of all N-cycle processes.

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