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Soil nitrogen levels are linked to decomposition enzyme activities along an urban-remote tropical forest gradient

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ABSTRACT

Urban areas in tropical regions are expanding rapidly, with significant potential to affect local ecosystem dynamics. In particular, nitrogen (N) availability may increase in urban-proximate forests because of atmospheric N deposition. Unlike temperate forests, many tropical forests on highly weathered soils have high background N availability, so plant growth is unlikely to respond to increased N inputs. However, microbial activity and decomposition of carbon-rich plant tissue can respond positively to added N in these forests, as has been observed in a growing number of fertilization studies. The relevance of these controlled studies to landscape-scale dynamics in urban-proximate moist tropical forests requires further investigation. I used ten forest stands in three watersheds along an urban-remote gradient in Puerto Rico to test the hypotheses that urban activity has a positive effect on soil N availability, and that decomposition enzyme activities vary with soil N. I found that mineral N, total dissolved N (TDN), and ammonium:nitrate (NH_4^+:NO_3^-) ratios varied by nearly one order of magnitude across the urban-remote gradient, and variability among urban sites was high. On average, urban forests had higher soil NO_3^-, lower NH_4^+, and lower C:N values than remote forests, suggesting high nitrification rates and/or external inputs of NO_3^- to the urban forests, and enrichment in N relative to C. Total mineral N and total dissolved N were positively correlated with the activities of enzymes that acquire carbon (C) and phosphorus (P) from organic matter. Across this gradient soil N levels were stronger predictors of enzyme activities than soil C or pH, which drive enzyme activities globally. The ratio of NH_4^+:NO_3^- was the strongest predictor of oxidative enzyme activities. Compared to global averages, ratios of C:N:P enzyme activities across these tropical forests indicated lower relative N-acquisition and higher relative P-acquisition, with N-acquisition lowest in the urban watershed, and P-acquisition highest in the upper-elevation remote watershed. These results suggest a strong urban effect on forest soil N levels, and show a link between changes in N availability and microbial processing of soil organic matter.

1. Introduction

Urban and industrial expansion are occurring rapidly in tropical regions (Lambin et al., 2003), with significant potential to alter biogeochemical processes in urban-proximate forests (Kaye et al., 2006; Martinelli et al., 2006). In particular, atmospheric nitrogen (N) deposition, until recently considered a North Temperate Zone problem, is expected to be highest in tropical regions in the coming decades (Galloway et al., 2004). Unlike many temperate forests, tropical forests on highly weathered soils tend to be rich in N, with high N availability and rapid rates of internal N cycling (Walker and Syers, 1976; Chestnut et al., 1999; Martinelli et al., 1999; Hedin et al., 2009). In temperate regions, urban-proximate forests can have higher soil N levels, mineralization rates, and N leaching relative to rural reference sites (White and McDonnell, 1988; Zhu and Carreiro, 1999; Groffman et al., 2009), providing an opportunity to assess human influences on the N cycle relative to background processes (Groffman et al., 2006). Similar urban-remote gradient studies are notably lacking for tropical ecosystems.

The extent to which added N may be retained in highly weathered tropical soils in urban-proximate forests is unknown. Because of high background soil N, deposition of this element in tropical regions could lead to large losses of N from soils, and lower retention than has been observed in temperate forests (Matson et al., 2002), such that soil N levels may not change drastically with N deposition. For example, an urban watershed in Puerto Rico showed large leaching losses of N compared with rural watersheds (Ortiz-Zayas et al., 2006). Even with large leaching losses and

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relatively low plant demand, however, ecosystems within tropical urban watersheds may retain added N. An N fertilization experiment in Hawai'i showed that added N can be retained in N-rich highly weathered soils, regardless of background N levels or plant demand, via sorption to charged mineral surfaces (Lohse and Matson, 2005). The retention of additional N in highly weathered, N-rich tropical soils near urban areas has yet to be examined at the landscape-scale.

Even in N-rich tropical forests, increased soil N availability has the potential to alter ecosystem dynamics. While N addition can stimulate plant growth in temperate forests (Townsend et al., 1996; Nadelhoffer et al., 1999; Churkina et al., 2010), a growing number of fertilization studies in N-rich tropical forests on highly weathered soils have demonstrated an apparent lack of N limitation to aboveground plant growth (Mirmanto et al., 1999; Harrington et al., 2001; Ostertag, 2001; Kaspari et al., 2008; Cusack et al., 2011b). Nonetheless, inputs of N to N-rich tropical forests have the potential to alter soil organic matter (SOM) cycling through a suite of microbially mediated mechanisms, including changes in decomposition enzyme activities, transport of dissolved organic C (DOC), and changes in soil respiration (Cleveland et al., 2006; Cleveland and Townsend, 2006; Mo et al., 2008; Cusack et al., 2010, 2011a, 2011b). Thus, changes in N availability in urban-proximate tropical forests may affect soil C storage and loss, with implications for global C cycling.

The sensitivity of microbial processes to added N in tropical forests is likely due in part to the high N:C requirements of decomposers relative to the range of N:C available in plant litter and soil organic matter (SOM) (Sylvia et al., 2004). However, N fertilization does not affect decomposition equally across sites (Berg and Matzner, 1997; Knorr et al., 2005), likely because of differences in litter tissue chemistry and varying responses to added N by different decomposition enzymes (Allison and Vitousek, 2004). For example, if N addition alleviates N limitation to decomposition, the activities of hydrolytic enzymes that acquire C and phosphorus (P) from organic matter are likely to increase, whereas enzymes that acquire N are likely to decrease (Sinsabaugh and Moorhead, 1994). Oxidative enzyme activities, which degrade complex C compounds and release physically occluded N, can also decrease with added N (Keyser et al., 1978; Fog, 1988; Carreiro et al., 2000; Cusack et al., 2010), particularly in lignin-rich litter (Waldrop et al., 2004). Thus, the net effect of increased N availability on decomposition enzyme activities depends on local substrate chemistry and the relative responses of different suites of enzymes.

I used ten forest sites along an urban-remote gradient in Puerto Rico to: (1) assess the urban influence on soil N levels, and (2) explore links between changes in soil N status and changes in decomposition enzyme activities. I hypothesized that urban-proximate tropical forests have elevated soil mineral N relative to remote forests, indicating retention of N deposition. I also hypothesized that soil mineral N levels are positively associated with the activity of enzymes that acquire C and P from SOM, but negatively associated with N acquisition and oxidative enzyme activities. I expected that ecosystem properties that drive enzyme activities in relatively undisturbed forests, such as soil C and pH (Sinsabaugh et al., 2008), would be secondary to mineral N in predictive power along an urban-remote gradient. Finally, I predicted that C:N:P ratios of acquisition activities would show lower relative N acquisition in forests closer to the urban center.

2. Materials and methods

2.1. Study sites

This study was conducted along an urban-remote forest gradient encompassing ten forest stands across three watersheds in Puerto Rico. Eight urban and suburban forest stands were located in the Rio Piedras watershed within the NSF San Juan Urban Long Term Research Area (ULTRA-Ex), with forest fragments spanning the watershed from the low-elevation urban core on the coast, to suburban areas in the upper watershed (Table 1). Two remote forests in a mid-elevation and an upper-elevation watershed in the Luquillo Experimental Forest, an NSF Long Term Ecological Research (LTER) site, were included (Fig. 1). Nitrogen fertilization experiments in both of the remote forests have demonstrated a lack of N-limitation to plant growth and litterfall productivity (Cusack et al., 2011b). Nitrogen deposition in the remote sites was ~3 kg-N ha^{-1} yr^{-1} (NADP/NTN, 2009). Sixteen weeks of preliminary N deposition data in the urban watershed showed high variability in N deposition rates, which when scaled up could represent inputs ranging from 10 to 40 kg-N ha^{-1} yr^{-1} (USFS-IITF 2011, unpublished data).

The Rio Piedras watershed is in the subtropical moist forest life zone (sensu (Holdridge et al., 1971)), ranges in elevation from 0 to 220 m above sea level (masl), has mean annual precipitation (MAP) of 1750 mm yr^{-1}, and mean annual temperature (MAT) of 25.7 °C. The Rio Piedras forests contain a mixture of native and non-native species, including exotic trees of the Fabaceae family in the canopy (Helmer, 2004; Lugo, 2004; Kennaway and Helmer, 2007). Forest fragment sizes, distance to urban center, and distance to the nearest major road were measured for urban forests using an Arc GIS land-cover classification map (Kennaway and Helmer, 2007, Table 1). Forest fragments were defined as areas of continuous forest, and were generally bounded by roads, grass sites or urban

Table 1
Site information is shown for eight urban forest stands (Urban), a mid-elevation remote forest (Mid-R), and an upper-elevation remote forest (Upper-R). Data are shown for forested sites within six urban sub-watersheds (1–6) feeding the main stem (0) of the Rio Piedras river. The second digit designates the tertiary tributary (e.g. 0.5). Urban sites are ordered from lowest elevation and closest proximity to the urban center (0), to highest elevation and farthest from the urban center (6). Exotic N-fixing trees in the canopy are shown as a percent of total basal area (mean ± 1 SE, $n = 3$).

Watershed	Site ID	Elevation masl	Latitude N	Longitude W	Forest fragment size km^2	Distance to urban center km	Shortest distance to major road km	Basal area m^2 ha^{-1}	Exotics % of basal area
Urban	0.5	20	18.4079	−66.0934	0.27	3.6	0.6	38 ± 1	84 ± 2
Urban	2.6	50	18.3813	−66.0420	1.79	7.4	1.4	29 ± 2	3 ± 3
Urban	3.0	40	18.3831	−66.0496	1.79	6.8	2.1	30 ± 2	9 ± 3
Urban	3.4	80	18.3662	−66.0539	0.08	8.3	1.6	14 ± 2	80 ± 8
Urban	4.3	100	18.3483	−66.0444	0.21	10.5	2.6	20 ± 3	18 ± 10
Urban	5.0	160	18.3349	−66.0394	0.56	12.1	1.2	29 ± 6	87 ± 6
Urban	5.1	120	18.3425	−66.0517	0.06	10.9	1.3	37 ± 9	69 ± 2
Urban	6.0	88	18.3453	−66.0718	0.07	10.3	0.2	33 ± 3	94 ± 4
Mid-R	RM	260	18.3138	−65.7443	[a]	~35	7.9	31 ± 4	0
Upper-R	RU	640	18.2845	−65.7880	[a]	~35	10.3	32 ± 5	0

[a] Remote forest sites were in the Luquillo Experimental Forest within El Yunque National Forest, which covers 11,270 ha.