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Urbanization Alters Soil Microbial Functioning in the Sonoran Desert

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Abstract

Cities can transform ecosystems in multiple ways, through modification of land use and land cover and through exposure to altered physical, chemical, and biological conditions characteristic of urban environments. We compared the multiple impacts of urbanization on microbial carbon (C) and nutrient cycling in ecosystems across Phoenix, Arizona, one of the fastest growing metropolitan areas in the USA. Land-use/land-cover change from desert to managed ecosystems altered soil microbial functioning, primarily through changes in organic matter supply. Although residential xeriscapes often feature native plants and patchy structure like deserts, spatial heterogeneity in soil biogeochemical cycling was not tightly linked to plant canopies. Grassy lawns exhibited higher nitrogen (N) and phosphorus demand by microorganisms than other landscape types, suggesting that high C quality may effectively sequester these nutrients during periods between fertilization events. Soils in native desert remnants exposed to the urban environment had higher organic matter content, but supported lower activities of extracellular peroxidase enzymes compared to outlying deserts. Experimental N enrichment of desert systems decreased peroxidase activities to a similar extent, suggesting that protected desert remnants within the city are receiving elevated N loads that are altering biogeochemical functioning. Although some microbial processes were spatially homogenized in urban desert remnants, resource islands associated with plants remain the dominant organizing factor for most soil properties. The extent to which native desert preserves within the city functionally resemble managed xeriscapes and lawns suggests that these remnant ecosystems are being 'domesticated' by exposure to the urban environment.

Key words: Sonoran Desert; EEA; peroxidase; lawn; xeriscape; fragmented ecosystems.

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Introduction

Warm desert ecosystems are characterized by patchy resource availability and environmental extremes that structure ecological communities. High temperatures and low precipitation generally limit biological processes, and productivity is organized heterogeneously around seasonal, episodic pulses of rainfall, topographic gradients that redistribute runoff, and plant canopies that capture and maintain pools of organic matter and

nutrients (Noy-Meir 1973; Virginia and Jarrell 1983; Martinez-Yrizar and others 1999; Reynolds and others 1999). Microbial activity in desert uplands is often stimulated by even brief rainfall events, but small carbon (C) pools in desert soils limit the duration of heterotrophic processes, particularly in poorly vegetated patches between shrubs and trees (Schaeffer and others 2003; Sponseller and Fisher 2008). Low organic matter content in desert soil is in part due to low productivity, but it may also be due to active loss pathways that are common in arid ecosystems and operate even under dry conditions. These losses include photodegradation and extended decomposition by microbial extracellular enzymes (EEA) that are stabilized by mineral surfaces and optimized by high soil pH (Gallo and others 2006; Stursova and Sinsabaugh 2008).

Humans have altered the structure of arid ecosystems historically and prehistorically through irrigation and fertilization for agriculture, grazing, and most recently, urbanization (Woodbury 1960; Jenerette and Wu 2001; Asner and others 2004; Grimm and Redman 2004; Wentz and others 2006). Currently, the arid US Southwest is experiencing the fastest population growth in the country, over thrice the national rate, led by cities in Arizona and Nevada (2.8–2.9% y^{-1}) (U.S. Census Bureau 2007). Although intensive grazing can accentuate resource islands (Schlesinger and others 1990), managed agriculture and urbanization may homogenize the magnitude, timing, and distribution of resources, through changes in land use and land cover, direct human management, or changes in the atmosphere or water on which these ecosystems depend. For example, monoculture turfgrass lawns associated with urban centers are now the largest irrigated crop in the USA, covering 13–20 million hectares and contributing to high rates of water and fertilizer use (Robbins and Birkenholtz 2003; Milesi and others 2005). In addition to lawns, alternative landscaping with drought tolerant or native desert plants is a common practice in arid US cities, but ecosystem processes in xeriscaped desert yards that have been restored from lawn landscapes likely differ from deserts despite their visual similarities (Davies 2008).

The urban environment may also alter ecosystem functioning through changes in trophic dynamics and diversity (Faeth and others 2005), atmospheric composition, and climate. For example, compared to their surroundings, urban ecosystems and their airsheds experience high concentrations of atmospheric carbon dioxide (CO_2) and ozone (O_3) (Wentz and others 2002; Atkinson-Palombo and others 2006), decreased wind speeds (Givoni 1998), altered humidity and high nighttime temperatures (Brazel and others 2000), and elevated rates of C and nitrogen (N) deposition (Lohse and others 2008). The effects of elevated CO_2, O_3, warming, and N deposition have been well studied in forests and grasslands (Aber and others 1998; Fenn and others 1998; Shaw and Harte 2001; Gregg and others 2003; Zak and others 2003), and CO_2 and N enrichment can alter numerous ecosystem processes, including nutrient cycling and organic matter utilization by soil microorganisms (Henry and others 2005b; Chung and others 2007; Menge and Field 2007). However, the combined impacts of the urban environment are not well understood in arid ecosystems or in native ecosystems that are embedded within the urban matrix. If urban atmospheric input is significant and microorganisms can utilize these compounds (Johnsen and Karlson 2007), the urban environment could diminish spatial patchiness of deserts by increasing available resources in C-poor spaces between shrub islands. Alternatively, because shrubs efficiently intercept aerosols (Schlesinger and Hasey 1980), the effect of urban deposition may be most evident under plants where nutrient accumulation is largest (McCrackin and others 2008). Additionally, the combined effects of elevated CO_2 and urban deposition may enhance existing resource islands by stimulating belowground production and microbial nutrient turnover beneath plant canopies, particularly during wet years when soil resources are abundant (Schaeffer and others 2007a; Shen and others 2008). For example, a recent study in arid grasslands of New Mexico found that experimental N additions increased spatial heterogeneity in microbial processes by enhancing C-acquiring cellulolytic enzyme activities in soils under grass tussocks and decreasing N-acquiring enzyme activities in cryptobiotic soils between plants (Stursova and others 2006).

In this study, we explored the consequences of urbanization on the magnitude and distribution of soil properties and microbial processes in a range of sites across the Phoenix metropolitan area. Our sites included native Sonoran Desert outside of the urban environment, native remnant desert within the urban core, residential yards xeriscaped with native and other drought-tolerant plants, and grassy lawns located in municipal parks. Furthermore, we explored the mechanisms responsible for urban impacts through an N-enrichment experiment in which we compared microbial activity in undisturbed desert plots with those that received

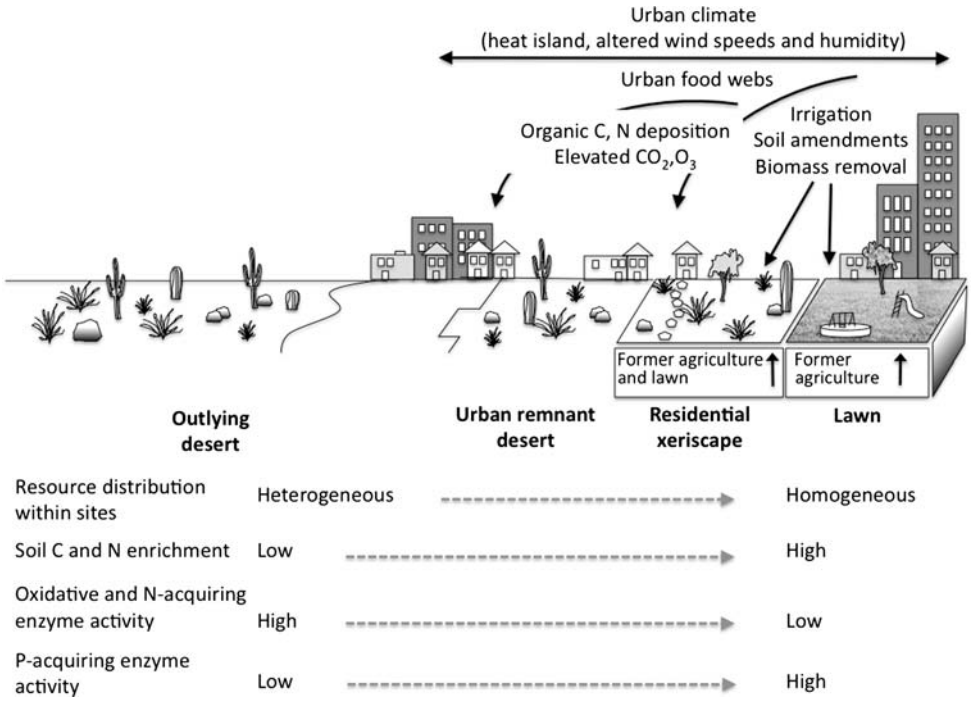

Figure 1. Hypothesized effects of the urban environment on soil resources in natural and managed landscapes. The four landscape categories shown are those sampled in this study. Note that urban managed landscapes bear distinct land-use histories as they overlie former agricultural fields (lawn sites) and both former agriculture and former lawn (residential xeriscape sites). The *gray, dashed arrows* represent hypothesized changes in soil resources with urbanization but do not imply that these changes will be linear.

supplemental N for 2 years. We expected that the effects of urbanization through land-cover and land-use change from desert to grassy lawns and residential xeriscaped yards would have large effects on the magnitude and distribution of soil microbial processes due to year-round management, land-use legacies, and rapid plant growth (Figure 1). We expected that the effects of urbanization through C and N enrichment of desert soil would be more subtle, but would increase microbial N cycling, decrease the activity of enzymes used by heterotrophic soil microorganisms for polyphenol degradation and N acquisition, and increase the activity of P-acquiring enzymes as N limitation is alleviated. Furthermore, we expected microbial processes would be homogenized across desert remnant landscapes within the city, diminishing resource islands associated with plant canopies (Figure 1).

Methods

Site Description

To test our hypotheses, we chose five replicate sites within four common land-use types in the Phoenix metropolitan area, including protected native Sonoran Desert sites outside of the urban core ('outlying desert'), protected native Sonoran Desert fragments within the urban core ('remnant desert'), managed residential yards landscaped with native and other drought-tolerant plant species ('xeriscape'), and municipal parks covered in fertilized, irrigated turfgrass ('lawn') (Figure 2). All sites were located within the 6,400-km^2 boundary of the Central Arizona–Phoenix Long-Term Ecological Research ecosystem (CAP LTER). Mean annual temperature in the Phoenix metropolitan area is 23°C and ranges from 12°C in winter to 34°C in summer (NOAA 2001). Annual average rainfall is 193 mm distributed bimodally through the year with approximately 35% as convective monsoon storms from June to September and approximately 65% from Pacific cyclonic storms between November and April (Western Regional Climate Center, www.wrcc.dri.edu). Land cover in the CAP LTER ecosystem is composed of Sonoran Desert vegetation (36%), lawn (11%; in residential, municipal/industrial, golf courses), managed xeric landscapes (13%; in residential, municipal/industrial, transportation corridors), agriculture (8%), bare ground (9%; in vacant lots, dirt roads), water (1%; in canals, streams), and impervious surface (22%).

Desert sites were chosen from all protected land within the CAP LTER using a stratified random design to control for abiotic state factors, plant species, and location relative to the city. All sites were on gentle slopes and located on geological substrates of mixed alluvium. Soils were hyperthermic Aridisols, which make up about 70% of the pedons across this landscape. McAuliffe (1994) has shown that creosote bush (*Larrea tridentata* (DC.)

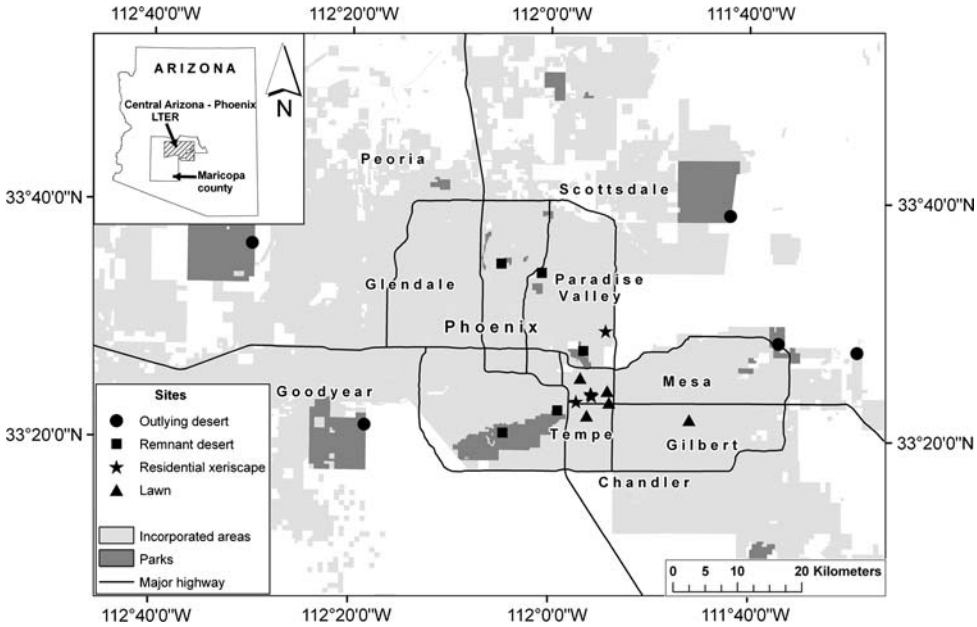

Figure 2. Map of the 20 sites used in this study, including 5 each of desert sites outside of the urban airshed ('Outlying desert'), remnant desert sites within the urban core ('Remnant desert'), xeriscaped residential yards ('Residential xeriscape'), and grassy municipal parks ('Lawn'). Each desert site contained a 20 m × 20 m control plot ('Ambient') and a plot of the same size that had been fertilized every 6 months over 2.5 years at 60 kg N ha^{-1} y^{-1} as ammonium nitrate (total 90 kg N ha^{-1} y^{-1} N applied over 2.5 years at the time of sampling; 'N-fertilized'). *Symbols* for three of the xeriscape sites are overlapping.

Coville) and bursage (*Ambrosia* spp.) in the Sonoran Desert occur together on soils that lack strongly developed argillic horizons that impede water infiltration and availability (McAuliffe 1994). Thus, to control for soil properties, we selected sites that included both *L. tridentata* and *Ambrosia* spp, including both white bursage (*Ambrosia dumosa* (A. Gray) Payne), and triangle-leaf bursage (*A. deltoidea.* (Torr.) Payne). Desert vegetation in our sites also included various cacti, such as saguaro (*Carnegiea gigantea* (Engelm.) Britton & Rose) and cholla (*Cylindropuntia* spp.), varying abundance of shrubs and trees (*Parkinsonia microphyllum* and *Prosopis juliflora*), and various herbaceous species (*Poa* spp., and *Boraginacea* spp.).

Previous studies in the Phoenix metropolitan area have shown that past land use significantly influences soil properties (Lewis and others 2006; Kaye and others 2008). Thus, residential xeriscaped and lawn sites were chosen from urbanized landscapes within the CAP LTER ecosystem using a stratified random design to control for current land use and land-use history. All grassy lawns located in municipal parks used currently for recreation were at least 19 years old, and were formerly agricultural fields. Residential xeriscaped yards were chosen to have a typical history for this land-use type in the metropolitan core: they were at least 5 years old, and they were predated by lawn for 10 or more years and agriculture prior to lawn for 20 or more years. Vegetation in lawn sites was dominated by Bermuda and rye grasses (*Cynodon dactylon* and *Lolium* spp.). Xeriscaped sites were diverse but all included plants native to the Sonoran Desert, including brittlebush (*Encelia farnosa* Gray ex. Torr.), palo verde (*Parkinsonia* spp.), as well as other common, non-native xeriscape shrubs (for example, *Leucophyllum* spp.), trees, and cacti.

Experimental Design

In each desert site, we sampled soils within one 20 m × 20 m plot that has never been fertilized ('ambient') and in one 20 m × 20 m plot that has been experimentally fertilized with N for 2.5 years as a part of a long-term experiment of the CAP LTER to assess nutrient limitation in perennial shrub communities (NH_4NO_3 as a solid, broadcast by hand at 60 kg N ha^{-1} y^{-1}, which is double the hypothesized rate of N deposition near urban centers in the western USA, 'N-fertilized'; Fenn and others 2003). Plots were fertilized twice per year after the first rainfall of the winter season (January) and once at the onset of the summer monsoon rains (July). Plots were chosen to include at least five individuals each of the two dominant

plant species used in our site selection criteria, *L. tridentata* and *Ambrosia* spp. Plots were also chosen to avoid inclusion of common leguminous trees. In each plot within the desert sites, we stratified our soil sampling by patch type, including under *L. tridentata* ('under plant') and in spaces between shrubs ('inter-plant space'). Because microbial activity in arid ecosystems attenuates quickly below the first several centimeters of soil (Noy-Meir 1973), three soil cores of 2-cm-depth per patch type were collected randomly in each desert site and homogenized.

Specific plots were not chosen within the xeriscape and lawn landscape categories because sites were already bound by impervious surface that delineated each residential yard (xeriscape category) or municipal park (lawn category). In each xeriscaped yard, we stratified our soil sampling by patch type similar to the design in desert sites, collecting soils from under established, mature *Encelia farinosa* ('under plant') and in spaces between shrubs covered with gravel (gravel was removed prior to sampling; 'inter-plant space'). Two soil cores of 2-cm-depth per patch type were collected randomly in each site and homogenized. Soil samples from lawns were composed of two cores of 5-cm-depth sampled randomly from grassy areas more than 10 m away from known trails/paths within each municipal park. Lawn soils were collected immediately prior to each assay, stored on ice, and analyzed within 24 h of collection (12–28% gravimetric moisture), whereas desert and xeriscaped soils were dry when collected and further air dried before analyses (0.4–1.5 and 0.7–3.3% gravimetric moisture for deserts and residential xeriscapes, respectively).

We compared soil samples among sites, assuming that any interannual or seasonal variation would affect all sites approximately equally, and that differences between landscape types are most likely to be detectable during the dry, pre-monsoon period. Thus, EEA, shaken-slurry nitrification potentials, and inorganic N pools were assayed using soils collected in June, 2007, prior to the summer monsoon rains (1–3% moisture for desert sites). Net potential rates of N mineralization and nitrification were also performed on desert and xeriscaped soils collected in June, 2007 and on lawn soils collected in March 2008. Because soil moisture in lawn soils is regulated by irrigation rather than rainfall and net N transformation rates were determined in laboratory incubations under controlled conditions, we compare these fluxes between landscape categories despite the difference in collection time. Denitrification enzyme assays were conducted and pH measured on soils from all sites collected in January 2008, more than 48 h after a rainfall event.

Soil Properties and Processes

In all soils, we measured a range of soil properties and processes including soil moisture, inorganic N concentration, pH, soil organic matter (SOM) content, and potential rates of net N mineralization and nitrification. Collected soils were homogenized and sieved to 2 mm in the laboratory. One 10-g subsample from each sample was immediately shaken for 1 h in 50 ml 2 N KCl, filtered through pre-leached Whatman #42 filters, and then frozen immediately for later analysis. Another 10-g subsample was placed in a small, capped cup and its water content was raised to 60% water-holding capacity with deionized water. These subsamples were placed in the dark for 8 days at 28°C. After the incubation, soils were extracted as described above. All KCl extracts were analyzed colorimetrically for NH_4^+–N and NO_3^-–N using a Lachat Quikchem 8000 autoanalyzer (Loveland, Colorado, USA). Potential net N mineralization was calculated as the difference between the sum of NH_4^+ and NO_3^- concentrations before and after each incubation. Potential net nitrification was calculated as the difference between NO_3^- concentrations before and after each incubation. Gravimetric soil water was determined by drying soil subsamples for 24 h at 105°C. SOM was estimated gravimetrically as mass lost following combustion for 4 h at 550°C.

Shaken-Slurry Nitrification Potential Assays

We used methods described in the study of Hart and others (1994) to assess potential nitrification rates in our soils using the shaken-slurry assay. Rates of potential nitrification using this assay have been used as an 'index' of nitrifier population size (Belser 1979; Hart and others 1994). An aliquot of 25 g of soil was added to flasks along with 100 ml of a solution containing 50 mM $(NH_4)_2SO_4$, 0.2 M K_2PO_4, 0.2 M KH_2PO_4, and adjusted to pH 7.2. Blanks of solution without soil were also processed at this time. Soil slurries were shaken vigorously on a mixer for 24 h at 23°C. At four times within this 24 h period, 10 ml aliquots of soil slurry were removed from the flasks, centrifuged, flocculated with a 0.6-M solution of $MgCl_2$ + $CaCl_2$ to aid in filtration, filtered through pre-leached Whatman #42 filters, and frozen until analysis. Extracts were analyzed colorimetrically for NO_3^- at on a Lachat autoanalyzer. Potential nitrification rate was

determined as the positive, linear slope of NO_3^- concentration in soil extracts over the 24-h period.

Denitrification Enzyme Assays

To assess potential rates of soil denitrification, we used methods described in the study of Groffman and others (1999). Approximately 50 g sieved soil was weighed into a 125-ml Wheaton bottle fitted with a rubber septum. An aliquot of 50 ml of incubation medium containing 100 mg N/l NO_3^- and 100 mg C/l as dextrose was added, and soil slurries were bubbled with N_2 to make the solution and flask headspace anaerobic. Capped bottles were amended with 10 ml acetylene (C_2H_2) and were incubated at room temperature (28°C) on a rotary shaker. Two 5 ml headspace samples were taken from each bottle, one at 5 min after C_2H_2 addition (initials), and one at 2.5 h (finals) in pre-evacuated vials. N_2O concentrations in headspace samples were determined using a gas chromatograph fitted with an electron capture detector and calibrated using certified N_2O standards in the laboratory. Potential denitrification rates for the 2.5-h period were measured from the increase in N_2O concentrations in the headspace plus the accumulation of dissolved N_2O estimated using the Bunsen absorption coefficient of dissolved N_2O in water at laboratory temperature (0.48 at 28°C) (Groffman and others 1999).

Extracellular Enzyme Activities

Soil samples from the desert and lawn sites were assayed for potential activities of eight extracellular enzymes at the University of New Mexico using protocols described in the study of Stursova and others (2006). These enzymes are important in C, N, and P acquisition by heterotrophic microorganisms and include phosphatase ('Phos', EC 3.1.3.1, 4-MUB-phosphate), leucyl aminopeptidase ('LAP', EC 3.4.11.1, L-leucine-7-amido-4-methylcoumarin), cellobiohydrolase ('CBH', EC 3.2.1.91, 4-MUB-β-D-cellobioside), β-glucosidase ('β-gluc', EC 3.2.1.21, 4-MUB-β-D-glucoside), β-*N*-acetylglucosaminidase ('NAG', EC 3.2.1.14, 4-MUB-*N*-acetyl-β-D-glucosaminide), β-D-xylosidase ('β-xylo', EC 3.2.1.37, 4-MUB-β-D-xyloside), peroxidase ('Perox', EC 1.11.1.7, L-3,4-dihydroxyphenylalanine and H_2O_2), and phenol oxidase ('Phenox', EC 1.10.3.2, L-3,4-dihydroxyphenylalanine). Assays were conducted on all soils in triplicate using buffers approximated for soil pH of our sites using 50 mM bicarbonate at pH 8.0. Enzyme activities are tightly correlated to SOM pools (Sinsabaugh and others 2005), which vary considerably across our sites. Thus, we assessed patterns in organic matter utilization as indicators of microbial community composition by normalizing EEA for SOM pools and reporting data as amount of substrate converted per unit time and mass of organic matter (nmol g organic matter^{-1} h^{-1}; Sinsabaugh and others 2008). The stoichiometry of EEAs has also been used to estimate microbial nutrient demand (Sinsabaugh and others 2008). Following Zeglin and others (2007), we approximated the ratios of C-acquiring to N-acquiring enzyme activities using the ratio of β-gluc:(LAP + NAG) and the ratio of C-acquiring to P-acquiring enzyme activities using the ratio of β-gluc:Phos.

Data Analysis

To preserve a balanced design for hypothesis tests, we explored the impacts of urbanization using all sites in a one-way ANOVA excluding N-fertilized plots and averaging over patch types (with landscape type as the fixed effect). Additionally, we evaluated the multiple effects of urbanization with two-way ANOVA including residential xeriscaped sites and both outlying and remnant desert sites (not fertilized), all of which were sampled explicitly for patch type (landscape type, patch type as fixed effects). Finally, we explored the effects of the urban environment and N enrichment on ecosystem pools and processes using three-way ANOVA with desert sites only. Here, landscape type (outlying, remnant), patch type (plant, inter-plant space), and N-fertilization (ambient, N-fertilized) were treated as fixed effects. To determine the relationship between soil properties and processes, correlation matrices were generated between all potential independent variables (Table 1). Those that did not show significant relationships were selected as independent variables for standard least-squares regression analyses.

To assess the combined responses of multiple enzymes involved in organic matter decomposition, factor analysis was applied to the correlation matrix of EEA (phenol oxidase activities were not used in the analysis because they were not significantly different than zero across most sites and treatments). Factors were extracted using the principal component analysis (PCA) method followed by a varimax rotation. Components with eigenvalues above 1 were retained in the analysis. In interpreting the rotated factor pattern, a variable was said to load on a given component if the factor loading was above 0.6 or less than −0.6. Multivariate analysis of variance (MANOVA) was used to determine the importance of landscape type, patch type, and N-fertilization as fixed effects in composing the significant principal factors. To

Table 1. Surface Soil Properties and Processes in Urban Landscapes, $N = 5$

Landscape type	Patch type	Tmt	SOM (%)		Extractable NH_4^+ ($\mu g\ N\ g^{-1}$)		Extractable NO_3^- ($\mu g\ N\ g^{-1}$)		Total inorganic N ($\mu g\ N\ g^{-1}$)		pH		Net potential N mineralization ($\mu g N\ g^{-1}\ d^{-1}$)		Net potential nitrification ($\mu g\ N\ g^{-1}\ d^{-1}$)		Nitrification potential ($ng\ N\ g^{-1}\ h^{-1}$)		Denitrification potential ($ng\ N\ g^{-1}\ h^{-1}$)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Outlying desert	IP	Amb	1.7	0.3	2.0	0.4	2.9	0.7	4.9	0.9	7.5	0.2	0.3	0.2	0.6	0.2	156.8	28.9	36.9	7.9
		N	1.9	0.3	27.6	4.5	6.2	1.4	12.2	2.7	7.6	0.4	1.9	0.8	3.8	1.1	–	–	15.7	3.8
	P	Amb	2.8	0.5	2.6	0.5	9.6	2.3	33.9	5.9	7.6	0.4	0.3	0.7	0.5	0.8	279.4	73.0	201.0	92.6
		N	2.9	0.5	37.3	11.9	37.1	11.5	74.5	16.6	7.9	0.4	1.7	1.1	4.7	1.1	–	–	177.1	57.9
Remnant desert	IP	Amb	2.3	0.1	4.8	1.4	4.1	1.2	8.9	1.9	7.8	0.4	0.6	0.4	1.1	0.5	191.9	31.7	49.3	13.7
		N	2.7	0.3	16.3	5.5	13.8	3.7	24.6	5.8	7.4	0.4	1.1	1.4	2.0	0.8	–	–	34.6	12.8
	P	Amb	3.5	0.3	7.7	3.5	16.8	5.4	30.0	8.2	7.4	0.5	1.6	0.2	2.5	0.5	372.0	18.5	279.7	127.6
		N	4.1	0.4	37.5	16.5	25.7	6.1	63.2	17.5	7.7	0.3	2.0[d]	0.8	5.5[d]	2.1	–	–	447.3	139.2
Residential xeriscape	IP	–	6.1	4.2	4.6	1.4	24.5	10.9	29.0	12.2	8.2	0.3	7.1	6.0	7.4	6.0	214.9	57.8	1503.4	1392.2
	P	–	5.1	2.7	4.3	1.4	71.4	44.2	75.7	45.4	7.9	0.3	−1.6	−2.3	−1.1	2.0	372.2	254.0	1511.1	717.0
Lawn	P	–	10.5	1.1	0.9	0.4	14.2	4.4	15.1	4.6	7.5	0.3	0.6[e]	2.8	0.6[e]	1.9	1524.0	513.0	2676.6	479.3
ANOVA results, P value																				
[a]Desert sites only	Landscape type		**<0.001**		0.40		0.15		0.25		0.81		0.67		0.54		–		**0.03**	
	Patch type		**<0.001**		0.15		**<0.001**		**<0.001**		0.87		0.44		0.14		–		**<0.001**	
	N-fertilization		0.28		**<0.001**		**<0.001**		**<0.001**		0.75		0.19		**<0.001**		–		0.47	
	Landscape × N-fertilization		0.58		**0.01**		0.73		0.02		0.64		0.35		**<0.05**		–		0.43	
[b]Desert + Xeriscape	Landscape type		0.31		0.47		**0.001**		**0.001**		0.29		0.73		0.74		0.45		**0.01**	
	Patch type		0.11		**0.47**		**0.002**		**0.001**		0.43		0.24		0.24		0.36		**0.01**	
	Landscape × patch		0.56		**0.59**		**0.54**		**0.24**		0.75		0.17		0.13		0.40		0.90	
[c]All sites	Landscape type		**<0.01**		**<0.01**		0.08		0.09		0.57		0.45		0.35		0.02		**<0.001**	

SE standard error, SOM soil organic matter, Amb Ambient, N N-fertilized, IP inter-plant space, P under plant, Bold indicates significance.
[a]*Desert sites analyzed using three-way ANOVA (landscape type, patch, and N-fertilization as fixed effects).*
[b]*Desert and xeriscaped sites analyzed together with a two-way ANOVA excluding N-fertilized plots (landscape type and patch type as fixed effects).*
[c]*All sites analyzed together using one-way ANOVA or Kruskal–Wallis non-parametric test (landscape type as fixed effect) excluding N-fertilized plots and using averages of patch types for desert and xeriscaped sites.*
[d]*Excluding one outlier in remnant desert (N-fertilized, under plant) that was >4 SE smaller than the mean shown.*
[e]*Net rates determined for lawn soils collected in March, 2008.*

determine the importance of soil properties for each of the PCA factors, correlation matrices were generated between all potential independent variables. Those that did not show significant relationships were selected for standard least-squares multiple regression analyses with PCA factors as dependent variables.

To test how land-use legacies influenced soil properties and processes in xeriscapes and lawns, we used correlation analyses to examine relationships between soil variables and the length of time each site spent under a particular land use (that is, time spent as xeriscape/lawn and minimum years spent as agriculture). For xeriscapes, the number of years as lawn and subsequently as xeriscape was calculated using information provided by homeowners and the construction date of the house according to the Maricopa County assessor (http://www.maricopa.gov/Assessor/). The minimum number of years of agricultural use prior to lawn or xeriscape was 22–76 years and was determined by a land-use database at the CAP LTER that includes land-use classifications collected in 1912, 1934, 1955, 1975, 1995, 2000, and 2005 (Moritz and others 1998; Redman and others 2005). Because of the 20-year gap between land-use classifications until 1995, the minimum possible number of years of agricultural use was calculated for each sampling site. Because exact dates of conversion from desert to agriculture were not available, some sites may have been agricultural fields for more years than were used in our analyses. We assumed that grassy lawns were established the year the municipal park was built.

All data with non-normal distributions were transformed prior to PCA, ANOVA, correlation, and regression analyses (log, square root, or reciprocal root) to satisfy linear model assumptions of normality and homoscedasticity. If transformations were not sufficient to satisfy assumptions, non-parametric statistics were used to determine significant differences between groups (Kruskal–Wallis one-way ANOVA by ranks or Mann–Whitney *U*-tests). All statistical tests were conducted using SPSS 16.0 for Mac.

Results

Effects of Urbanization on Soil Properties and Processes

Land-use and land-cover change associated with urbanization had important effects on soil properties and microbial processes. Ecosystem processes between replicate, residential xeriscaped yards were highly variable, with large coefficients of variation for most variables associated with C and N

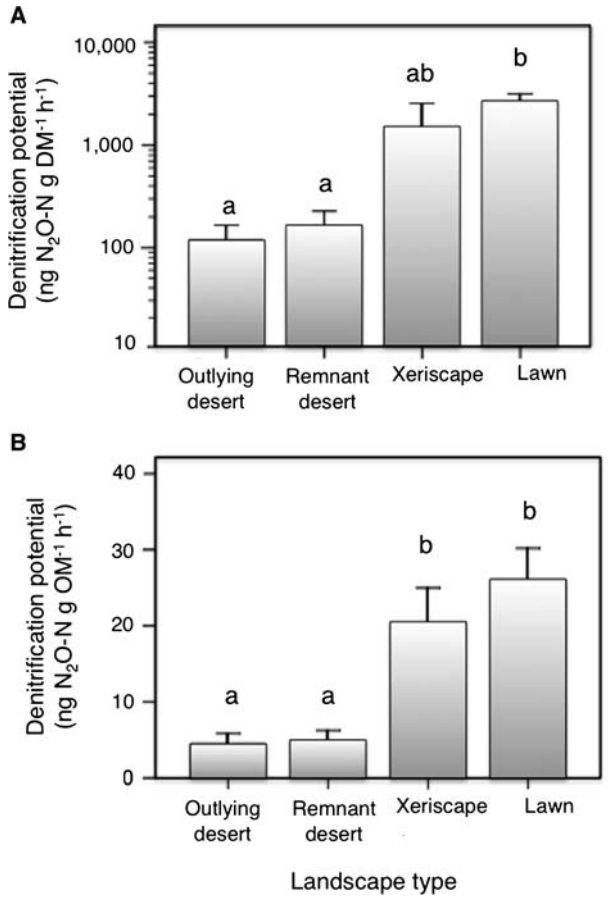

Figure 3. **A** Soil denitrification potential based on dry soil mass (DM) (ng N_2O–N g DM^{-1} h^{-1}). Note that the log-scale of the *y*-axis does not start at 0. **B** Soil denitrification potential standardized by organic matter content (OM) (ng N_2O–N g OM^{-1} h^{-1}). *Bars* represent mean values averaged across patch types, $N = 5$; error bars are ±SE. *Lowercase letters* represent significant differences between landscape types derived from one-way ANOVA with post hoc Tukey analyses.

cycling (Table 1). Nevertheless, on average they contained similar concentrations of inorganic N as remnant deserts but higher concentrations than their native desert counterparts outside the urban environment (Table 1; outlying < remnant desert = xeriscape, two-way ANOVA with post hoc Tukey, $P < 0.05$). Residential xeriscapes also resembled both remnant deserts and lawns in their potential to denitrify (on a dry mass basis; Figure 3A). Lawns had different soil characteristics and rates of nutrient cycling compared to xeriscapes or deserts, including significantly higher rates of nitrification than xeriscapes and larger pools of SOM than xeriscapes or deserts (Table 1; one-way ANOVA with post hoc Tukey, $P < 0.05$). In a multiple regression using non-correlated soil variables from Table 1 averaged across patch types

and excluding N-fertilized plots (SOM, ammonium and nitrate concentration, and pH), differences in rates of potential denitrification between lawns and other landscape types were largely driven by the differences in SOM pools (least-squares linear regression, SOM × log denitrification (ng N_2O–N g dry mass^{-1} h^{-1}); $r^2 = 0.68$, $P < 0.001$). However, when standardized by organic matter content across landscape types (μg N_2O–N g organic matter^{-1} h^{-1}), denitrification in managed urban landscapes such as lawns and xeriscapes was higher than in desert ecosystems but not different from one another (Figure 3B).

Urbanization has also altered properties and processes in soils of the Sonoran Desert through exposure to the urban environment. In a three-way ANOVA using desert sites only, SOM pools were larger in remnant deserts compared to outlying deserts, driven primarily by differences in inter-plant spaces (Table 1). Increased SOM content of remnant deserts was associated with decreased sensitivity to N enrichment. In other words, inorganic N pools and rates of net potential nitrification were enhanced by N-fertilization to a larger extent in outlying compared to remnant desert sites (significant landscape type × N-fertilization interaction; Table 1). Similarly, remnant deserts supported higher rates of potential denitrification per unit of dry soil than outlying deserts (Table 1, three-way ANOVA, remnant desert > outlying desert, $P = 0.03$), and rates of denitrification were more strongly related to SOM content than nitrate (least-squares regression, log [denitrification] × SOM, $r^2 = 0.38$, $P < 0.001$; log [denitrification] × SOM and nitrate, $r^2 = 0.45$, $P < 0.001$). When averaged across patch types and analyzed with other landscapes, however, rates of potential denitrification were similar between desert types (Figure 3). In contrast, presence or absence of plants played a larger role in explaining relative population sizes of nitrifying microorganisms and pools of extractable inorganic N in desert soils than exposure to the urban environment, and an equal role to the urban environment in explaining rates of potential denitrification and SOM content. Neither landscape nor patch type affected net rates of N mineralization, nitrification, or pH (Table 1).

Effects of Urbanization on EEA

In a PCA of ligninolytic and cellulolytic enzyme activities (standardized for SOM; β-gluc, β-xylo, CBH, Perox) in soils from different landscapes across the Phoenix metropolitan area, 86% of the variance in these variables was explained by two primary factors (Table 2; Figure 4). Factor 1 was associated with the hydrolases, β-gluc, β-xylo, and CBH, and Factor 2 was associated with peroxidase. In a multiple regression using non-correlated soil variables from Table 1 as independent variables (SOM, ammonium and nitrate concentrations, and pH) against each principal component, factor 1 was not significantly associated with any soil properties, but factor 2 was associated with SOM content ($r^2 = 0.30$, $P < 0.001$, $n = 45$), with lawn soils

Table 2. PCAs of EEA and MANOVA Results

Cellulolytic and ligninolytic enzymes			N-acquring and P-acquring enzymes		
	Factor 1	Factor 2		Factor 1	Factor 2
Enzyme, factor loadings					
β-gluc	**0.84**	0.24	NAG	−0.15	**0.98**
β-xylo	**0.96**	−0.56	LAP	**0.84**	−0.40
CBH	**0.88**	−0.22	Phos	**0.92**	0.21
Perox	−0.20	**0.98**			
Eigenvalue	2.39	1.07		1.61	1.10
Fraction of variance explained (%)	59.8	26.6		53.5	36.7
MANOVA results, *P* value					
Landscape type	0.54	**<0.001**		**<0.01**	0.51
Patch type	**0.02**	0.15		**<0.01**	**<0.001**
N-fertilization	0.50	**0.04**		0.75	0.68
Landscape × patch	0.06	0.15		0.19	0.11

Bold indicates significance.
Cellulolytic/ligninolytic enzymes and N-acquiring/P-acquiring enzymes analyzed separately.

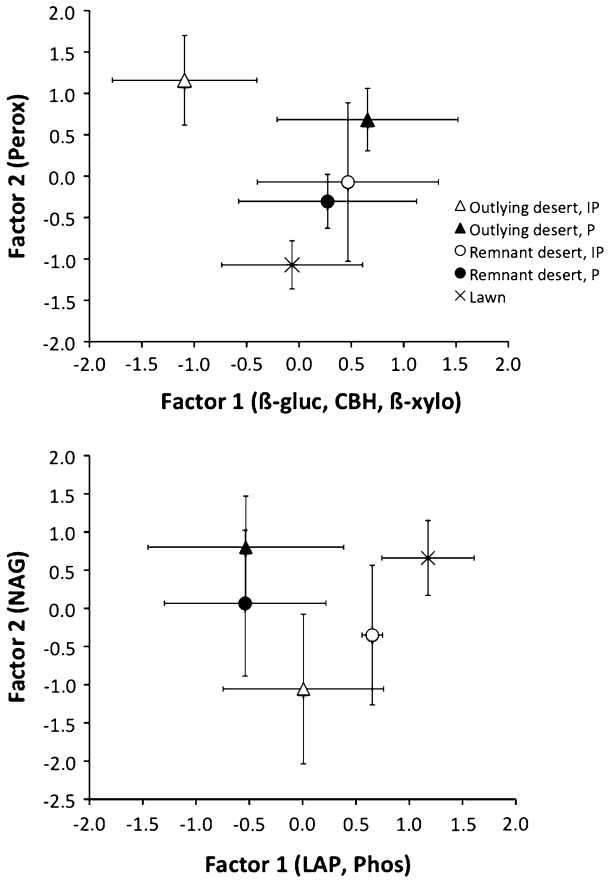

Figure 4. PCA of EEA at all sites. Bivariate plots of significant components from separate analyses using (**A**) ligninocellulolytic enzymes (β-gluc, β-xylo, CBH, and Perox) and (**B**) N- and P-acquiring enzymes (LAP, NAG, and Phos). *IP* inter-plant space, *P* under plants. *Symbols* represent mean factor scores for each landscape and patch, and *bars* represent 95% confidence intervals. N-fertilized plots not shown. See Table 2 for factor loadings and statistics for each axis.

falling at the highest values and outlying desert, inter-plant space soils at the lowest values on this axis (Figure 4). MANOVA with both factors as dependent variables showed that ligninolytic activity varied by landscape position ($P < 0.001$) and patch type ($P = 0.007$), but patch type was only significant in outlying deserts (landscape × patch interaction; $P = 0.04$). Tests of between-subject effects showed that landscape position (outlying > remnant = lawn) and N-fertilization (N-fertilization < ambient) varied significantly with factor 2 (peroxidase), whereas factor 1 (β-gluc, β-xylo, CBH) was explained by patch type (under plants > inter-plant space) (Table 2).

In a separate PCA, SOM-standardized N-acquiring and P-acquiring enzyme activity (LAP, NAG, and Phos) was condensed into two factors that explained 90% of the variation in these variables. Factor 1 was positively associated with the protein-degrading enzyme LAP and the P-acquiring enzyme, phosphatase, whereas Factor 2 was associated with the chitin-degrading enzyme, NAG (Table 2; Figure 4). In a multiple regression using non-correlated soil variables from Table 1 (SOM, ammonium and nitrate concentrations, and pH), both factors 1 and 2 were significantly but weakly related to extractable NO_3^- and SOM (Factor 1: $r^2 = 0.24$, $P < 0.01$, $n = 45$; Factor 2: $r^2 = 0.21$, $P < 0.01$, $n = 45$). Results of MANOVA showed that landscape type ($P < 0.05$) and patch type ($P < 0.001$) best explained the pattern of N-acquiring and P-acquiring enzymes in these urban soils. Tests of between-subject effects showed that factor 1 (LAP, Phos) varied by landscape type (lawn > outlying = remnant) and patch type (inter-plant space > under plants), whereas patch type alone was significant along factor 2 (NAG; under plants > inter-plant space) (Table 2).

Exposure to the urban environment was associated with changes in microbial organic matter utilization in desert ecosystems. Urban remnant desert soils contained less than half the activity of the lignin-degrading enzyme, peroxidase, than outlying desert soils both in inter-plant spaces and under plants (Table 3). Additionally, microbial organic matter utilization was more homogeneous across patch types in remnant deserts, diminishing the strong differences between plant and inter-plant spaces characterizing resource islands of arid ecosystems (Figure 4A). For example, activity of β-glucosidase, a cellulolytic enzyme, was higher under plants than in inter-plant spaces in outlying deserts, but was equal across patch types in remnant deserts (landscape type × patch type interaction; Table 3). Similar patterns were observed for β-xylo and NAG, although the trends were not significant at $P \leq 0.05$ (interaction between landscape type and patch type, $P = 0.08$ and 0.07, respectively). Furthermore, when analyzed separately within each region (due to use of non-parametric Mann–Whitney *U*-test, see below), the ratio of C-acquiring to N-acquiring enzyme activity was significantly higher under plants than in inter-plant spaces in outlying deserts ($P < 0.01$), but not in remnant deserts ($P = 0.18$).

Patch type was more important than the urban environment in explaining differences in most of the other hydrolases, including CBH, β-xylo, NAG, and LAP. In a three-way ANOVA in desert sites only, exposure to the urban environment did not have a significant effect on the ratio of C-acquiring to P-acquiring enzymes (β-gluc:Phos, $P = 0.44$),

but patch type was an important predictor of this ratio (under plants > away from plants; $P < 0.001$). ANOVA was not used on the ratio of C-acquiring to N-acquiring enzymes (β-gluc:[LAP + NAG]), because variances were heteroscedastic between desert types even after transformation; however, non-parametric Mann–Whitney *U*-tests on β-gluc:[LAP + NAG] within desert patch types showed no differences between urban and outlying desert sites ($P = 0.18$).

As expected, creation of intensively managed landscapes such as lawns also had large impacts on organic matter utilization by soil microorganisms. Lawn soils supported significantly lower SOM-standardized activities of ligninolytic enzymes than outlying desert soils but were similar to remnant desert soils (peroxidase; outlying desert > remnant desert = lawn). However, phosphatase activities were higher in lawns compared to all desert soils, a pattern supported by both ANOVA and PCAs (Table 3, Figure 4B). Patterns for the C-acquiring hydrolases were mixed: lawns supported significantly larger activities of CBH than outlying deserts (but similar to remnant deserts) and lower activities of β-gluc than either outlying or remnant deserts. The ratio of C-acquiring to P-acquiring enzymes and C-acquiring to N-acquiring enzymes was significantly higher in desert compared to lawn sites but not different between outlying and urban locations (outlying desert = remnant desert > lawn).

Effects of Land-Use History

Lawn age varied across the five replicates in our study, ranging from 19 to 55 years since park establishment. In a correlation analysis between soil variables and land-use history variables (time in current landscape, minimum years in agriculture), lawn age was significantly and positively correlated with the SOM-standardized activities of the N-acquiring enzyme LAP (Pearson's correlation, log [LAP] × lawn age; $r = 0.93$, $P = 0.02$) and the P-acquiring enzyme Phos (log [Phos] × lawn age; $r = 0.93$, $P = 0.03$). However, relationships between enzyme activities and lawn age were not due to patterns in SOM content (Pearson's correlation, lawn age × SOM; $r = 0.42$, $P = 0.48$) nor other soil properties. Minimum years of agriculture prior to lawn were not significantly correlated with any soil variables.

Age of xeriscaped yards ranged from 5 to 31 years, and the time these yards were landscaped in lawn prior to xeriscaping ranged from 13 to 44 years. In a correlation analysis between patch-averaged soil variables and land-use history variables (time in current landscape, minimum years in agriculture), concentrations of inorganic N were positively associated with the age of xeriscaped yards (Pearson's correlation: reciprocal root $[NH_4^+]$ × log [landscape age], $r = -0.97$, $P < 0.01$; reciprocal root $[NO_3^-]$ × log [landscape age], $r = -0.97$, $P < 0.01$). Minimum years of agriculture prior to lawn or xeriscape were not significantly correlated with any soil properties.

Effects of N Enrichment in Sonoran Desert Ecosystems

N additions increased pools of inorganic N and rates of potential net nitrification only in desert soils outside of the urban airshed and had little impact on SOM, pH, or potential net N mineralization (Table 1). Additionally, N additions had no effect on denitrification on a dry mass basis, but fertilization significantly decreased potential rates of denitrification when standardized for organic matter in inter-plant spaces (three-way ANOVA, patch × N-fertilization interaction, $P = 0.04$). N additions had no effect on individual EEA (Table 2). However, in a MANOVA using the ligninocellulolytic factors 1 and 2 as dependent variables, N-fertilization was significantly and negatively related to factor 2, which was composed of the peroxidase enzyme alone. N additions had no effect on the ratio of C-acquiring to N-acquiring enzyme activities or C-acquiring to P-acquiring enzyme activities.

Discussion

Urbanization in the Sonoran Desert within and around the Phoenix metropolitan area has altered soil processes both through land-cover and land-use change and through exposure to the urban environment. Additionally, although urbanization has homogenized the spatial distribution of some microbial processes, particularly in managed landscapes, resource islands associated with plants remain the dominant organizing factor for most soil properties in outlying and remnant native desert ecosystems.

Land-Use/Land-Cover Change

Urbanization altered soil properties and microbial functioning through changes in land use and land cover, primarily mediated by alterations in C and N supply. Residential xeriscaped yards in the urban core contained native plant species and were landscaped heterogeneously to resemble desert ecosystems, but they were functionally distinct from their native counterparts, resembling both

Table 3. EEA (nmol g organic matter^{-1} h^{-1}) and Results from ANOVA

Landscape type	Patch type	Tmt	β-gluc		CBH		β-Xylo		LAP		NAG		Phos		Perox		Phenox	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Outlying desert	IP	Amb	721	68	26	5	147	31	7575	1544	26	6	986	169	82880	12433	4030	3218
		N	913	187	37	5	158	16	7905	1679	31	1	1045	183	70120	12592	12020	8015
	P	Amb	1441	251	108	30	265	37	3962	703	57	8	980	225	60820	8296	12240	5555
		N	1338	287	95	27	248	49	4920	1233	64	9	958	258	49000	7909	12330	12198
Remnant desert	IP	Amb	1328	206	71	16	289	48	9661	887	38	6	1212	87	36720	11930	16410	6871
		N	927	183	47	12	196	34	9455	818	28	3	1017	114	14900	9599	3040	3044
	P	Amb	1042	135	83	18	260	36	5056	1147	45	11	797	158	27430	5570	1400	1402
		N	1131	271	110	31	253	56	3991	1424	47	6	735	243	22670	6915	2510	2513
Lawn	–	–	544	92	142	24	222	29	6024	650	43	5	3364	403	19420	3208	3760	1781
ANOVA results, *P* value																		
[a]Desert sites only	Landscape type		0.84		0.17		0.09		0.32		0.38		0.74		**<0.001**		0.61	
	Patch type		0.61		**<0.001**		**0.02**		**<0.001**		**<0.001**		0.09		0.58		0.42	
	N-fertilization		0.60		0.82		0.42		0.92		0.71		0.62		0.07		0.19	
	Landscape × patch		**0.05**		0.14		0.08		0.30		0.07		0.25		0.13		0.23	
[b]All sites	Landscape type		**0.01**		**0.03**		0.20		0.36		0.98		**<0.001**		**<0.001**		0.41	

IP inter-plant space, P under plants, Amb ambient (no fertilization), N N-fertilized, β-gluc β-glucosidase, NAG β-N-ace1ylglucosaminidase, CBH cellobiohydrase, Phenox phenol oxidase, Perox peroxidase, LAP leucyl aminopeptidase, β-xylo β-D-xylosidase.

[a]*Desert sites analyzed using three-way ANOVA (landscape type, patch type, and N-fertilization as fixed effects).*

[b]*Desert and lawn sites analyzed together using a one-way ANOVA (landscape type as fixed effect) exculding N-fertilized plots and using averages of patch types for desert sites.*

deserts and lawns. For example, rates of potential denitrification in xeriscapes were similar to lawns when standardized for organic matter content, which suggests that soil C quality is significantly higher in residential, restored desert yards compared to native desert systems. Also, despite restoration of patchy biotic structure in xeriscaped yards, SOM content and microbial processes of nitrification and denitrification were not associated with shrub canopies but instead were homogeneously distributed across patch types. Recent research in these sites suggests that changes in microbial activity and lack of resource islands have less to do with plant species (we sampled under *E. farinosa* in xeriscaped sites and under *L. tridentata* in desert sites) or plant size, but may be more related to agricultural land-use history that persists for decades within soil nutrient pools, as the yards sampled in this study were predated by both agriculture then by lawn (Lewis and others 2006; Davies 2008). Also, although they differ markedly in their structure, xeriscapes and lawns share characteristics related to management, including biomass removal (pruning in xeriscapes; mowing in lawns), soil amendments (herbicides in xeriscapes; fertilizers in lawns), and irrigation (drip irrigation in xeriscapes; sprinkler or flood in lawns) (Figure 1). These practices may serve to decrease resource islands associated with shrub canopies within yards but likely increase variability in processes between yards as management and yard structure vary with homeowner preferences (Larsen and Harlan 2006; Davies 2008). Furthermore, average soil inorganic N concentrations were positively related to yard age, suggesting that impacts of management on xeriscaped soils may aggrade over time.

As expected, lawns showed the largest differences in soil properties compared to native desert landscapes, with larger SOM pools and rates of nitrification and denitrification. However, we were surprised to find lower concentrations of inorganic N in lawns relative to other arid urban landscapes in contrast to our initial predictions (Figure 1), despite regular nutrient supplements from active management in these sites. N losses from lawns are likely higher than from desert and other residential landscapes (Guillard and Kopp 2004; Kaye and others 2004; Zhu and others 2004; Hall and others 2008), and large SOM pools, microbial populations, and active plant growth may limit the availability of extractable inorganic N in lawn soils, particularly between fertilization events. Supporting this premise, microbial communities in lawn soils had high P demand (high phosphatase activity was significantly associated with SOM content), lower peroxidase activities, and lower ratios of C-acquiring:N-acquiring and C-acquiring:P-acquiring enzymes than deserts, suggesting that microbial growth within lawns may not be limited as much by C as by N and P availability. Lawns sampled in this study likely carry an agricultural legacy within soil nutrient pools (Lewis and others 2006). However, we found strong, positive correlations between lawn age, LAP, and phosphatase activities but no relationship with total SOM content, suggesting that increases in C quality with lawn age may keep microbial N and P demand high.

Effects of the Urban Environment

Soils in the Phoenix metropolitan area were also altered by the urban environment, particularly those properties and processes associated with C cycling, although patch type remained the dominant organizing factor for other variables related to N availability. For example, in support of our hypotheses, soil C concentrations were larger in desert ecosystems within the city compared to deserts outside of the city, with nearly double the SOM content in inter-shrub spaces that reached concentrations comparable in size to outlying desert shrub islands. Furthermore, SOM content was strongly associated with heterotrophic microbial activity, leading to increased rates of denitrification and altered patterns of organic matter utilization in urban remnant compared to outlying desert sites.

SOM pools in temperate, mesic ecosystems are controlled to a large extent by the relative balance between production and microbial decomposition (Parton and others 1987). However, in arid ecosystems, SOM content may be regulated more by oxidative enzyme activities that are optimized at high pH and stabilized by mineral surfaces in dry soil (Sinsabaugh and others 2008; Stursova and Sinsabaugh 2008). We measured lower activities of organic matter-standardized peroxidase in soils of urban remnant deserts compared to outlying deserts despite similarities in soil pH between sites. Peroxidase and other oxidative enzymes have multiple sources in ecological systems, used within cells by plants and microorganisms to prevent oxidative stress and to defend against herbivores or pathogens, and used outside of cells for nutrient acquisition by fungi and some bacteria (Miller and others 2004; Rabinovich and others 2004; Balakrishnan and others 2007; Valencia-Islas and others 2007). Once in the soil, however, they can collectively catalyze the degradation of polyphenolic compounds (Sinsabaugh and others 2002a).

Although sources of these enzymes could differ across the study area, we do not anticipate that UV exposure differed systematically between our sites, nor was there evidence that plant-derived enzymes drove the observed patterns, as we did not find significant differences in peroxidase activities between vegetated and un-vegetated patches. Recent study in the CAP LTER shows that root colonization of shrubs and succulents by arbuscular mycorrhizal fungi is lower in remnant desert parks compared to outlying deserts (Ontiveros-Valencia and Stutz 2009), and N-fertilization has been shown to decrease fungal biomass in other ecosystems (Wallenstein and others 2006). Our data suggest that factors within the urban environment may lead to the accumulation of recalcitrant organic matter in arid urban soils, possibly due to abiotic alteration of polyphenol availability (Lucas and others 2007) or changes in the structure of microbial communities responsible for lignin degradation.

The combined effects of elevated CO_2, air temperatures, and N deposition within the urban environment could also lead to our observed patterns in soil C and microbial functioning through changes in production and litter quality in desert remnant plant communities. For example, although results depend significantly on photosynthetic capacity and nutrient dynamics within ecosystem types, elevated CO_2 in forested ecosystems generally enhances heterotrophic microbial activity and C-acquiring EEA in the short term through increased quantity and quality of C compounds released by root systems (Zak and others 2003; Hickler and others 2008). Fewer studies have tested the impacts of the urban atmosphere in deserts, but recent evidence shows similar patterns, particularly during wet years when soil resources are abundant (Billings and others 2002; Schaeffer and others 2003; Phillips and others 2006). Similarly, in our study, remnant desert soils supported higher SOM-standardized activities of cellobiohydrolase than outlying deserts, with rates that were similar in magnitude to fertilized and irrigated lawns. Increased ratios of cellulolytic to oxidative enzyme activities are a common response to CO_2 or N enrichment in other ecosystems due to increased quantity of labile C compounds released by root systems or changes in fungal community composition and activity (Larson and others 2002; Sinsabaugh and others 2002b; Waldrop and Zak 2006; Chung and others 2007; Jin and Evans 2007; Schaeffer and others 2007b).

Although feedbacks from elevated CO_2 or N enrichment through shrub production may enhance C supply or quality under plant canopies (Jin and Evans 2007), this mechanism is less useful in explaining larger SOM content between plants or spatial homogenization of enzyme activities between patch types in our remnant desert sites. In addition to stimulating shrub production during wet years, the urban environment may also increase labile C pools in desert soils by altering composition or production of short-lived annual plants that grow both beneath and between shrub canopies. Modeling results for the Sonoran Desert suggest that winter C3 annuals will be more responsive to the urban atmosphere than shrubs (Shen and others 2008), and both CO_2 and N enrichment have been shown to affect the composition of herbaceous plant communities in other ecosystems (Reich and others 2001). Changes in tissue chemistry within species or species assemblages can feed back to significantly alter community litter quality (Henry and others 2005a), which could lead to higher ratios of cellulolytic to oxidative enzyme activities in our remnant desert sites.

Finally, other factors could contribute to increased SOM pools and possible homogenization of enzyme activities in remnant desert soils within the urban matrix, particularly in the typically low-C spaces between shrubs. The urban environment could increase organic matter pools and quality through enhanced populations of mammalian herbivores such as rabbits and rodents, particularly if consumed plant biomass were redistributed to inter-shrub spaces (Randa and Yunger 2006; Rytwinski and Fahrig 2007). Additionally, cryptobiotic crust communities within the urban core likely have been protected from grazing longer than outlying desert as urban land uses in Phoenix developed historically from the city center (Gober 2006). However, protection of surface soils from grazing may be offset by increased foot traffic likely received by these urban desert parks compared to outlying desert areas. Cities also emit a range of reduced C compounds to the atmosphere that could be deposited to soils and increase organic matter pools in inter-plant spaces (Seinfeld 1989). Rates of urban C deposition to soils have not been well studied, but recent studies in Phoenix estimated that 0–1.6 g organic C m^{-2} was added to soils annually (Lohse and others 2008; Kaye and others in preparation), representing a significant fraction of annual net primary production to low-C patches between shrubs in this desert ecosystem (ANPP 11–230 g m^{-2} y^{-1}; Shen and others 2005). However, in a related study, Kaye and others (in preparation) found that only fine particulate C from the Phoenix atmosphere was labile to soil

microorganisms, and this particle type composed only a small fraction of total C deposition to our sites.

Experimental N enrichment significantly increased rates of nitrification and inorganic N concentrations only in soils that were outside of the Phoenix airshed, suggesting that within the Phoenix metropolitan area urbanization has already increased N loading to desert ecosystems. This conclusion is also supported by PCAs showing that N additions decrease peroxidase activities in desert sites. N enrichment has been shown to decrease ligninolytic enzyme activities in temperate forest soils, but it had no effect on oxidases in fungal-dominated, semi-arid grasslands where oxidative enzyme activities are among the highest rates studied (Stursova and others 2006; Sinsabaugh and others 2008). Stursova and others (2006) suggest that oxidative enzyme production in arid ecosystems may be insensitive to significant changes in N supply because concentrations of inorganic N are commonly high, often accumulating on soil surfaces during long dry periods from deposition and asynchrony in microbial N mineralization and immobilization (Welter and others 2005; Stursova and others 2006; Collins and others 2008). Sonoran Desert soils examined in this study supported oxidative enzyme activities that were one to two orders of magnitude lower than in other arid and semi-arid systems (Sinsabaugh and others 2008) and may support soil microbial communities that are more sensitive to N enrichment.

Conclusions

Results from this study suggest that microbial processes in arid soils are responsive to human activities both through creation of managed urban landscapes and through factors associated with the urban environment that increase C and N supply. Urbanization homogenized soil biogeochemical cycling at the plant-interplant scale, most clearly observed within managed landscapes, but it increased heterogeneity at larger, neighborhood scales between yards, likely due to differences in management practices and preferences between households. Furthermore, xeriscaped yards and lawns within the Phoenix metropolitan area more closely resembled urban remnant deserts than outlying native desert landscapes in their biogeochemistry. Studies of arthropods and birds within the Phoenix metropolitan area show similar trends, with communities in remnant desert parks resembling more closely those in irrigated, mesic residential landscapes than outlying desert ecosystems (Shochat and others 2004; Faeth and others 2005). These patterns suggesting that remnant desert patches within the city core are being 'domesticated' by exposure to the urban environment.

High rates of population growth in arid and semi-arid regions are expected to intensify demands for scarce water resources that sustain both human populations and ecological communities. Our study suggests that biogeochemical cycling within protected, native ecosystems on the urban–desert interface will be altered by numerous factors associated with human settlements, including atmospheric nutrient enrichment. Conservation efforts to preserve biodiversity have traditionally focused on protection of wildlands to prevent development or other direct human use. However, a recent study suggests that 88% of protected areas worldwide are now likely to be impacted by urban growth (McDonald and others 2008). Thus, effective conservation in the 21st century will require studies that explicitly focus on the maintenance and improvement of ecological processes within human-dominated landscapes and their surroundings (Western 2000; Robinson 2006).

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