

Decaying woodrat (*Neotoma* spp.) middens increase soil resources and accelerate decomposition of contemporary litter

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ABSTRACT

Ecosystem engineers can have broad-reaching impacts when they alter biogeochemical pools and processes, thus affecting resource availability. In the Chihuahuan Desert, woodrats (*Neotoma* spp.) build stick nests on the soil surface within *Yucca baccata* patches. We assessed the impacts of these middens on the underlying soil pools. We also assessed midden impacts on litter decomposition because decomposition exerts control over soil biogeochemical pools. We specifically focused on midden activity state, selecting *Yucca* patches with no midden, an active midden, or a decayed midden. Soil were analyzed for organic carbon, total nitrogen, and available nitrogen. To probe a mechanistic driver of soil biogeochemical pools, we measured litter mass loss of mesquite leaflets (*Prosopis glandulosa*) and poplar wood (*Populus* spp.). Soil organic carbon, total nitrogen, available nitrogen and litter decay were all enhanced in decayed midden patches. These results support observations from other species in which the environmental modifications caused by ecosystem engineers persist beyond the life of the engineer. However, in this case the impacts of ecosystem engineers on biogeochemical pools and processes were greater for engineered structures that were not being maintained than for actively maintained structures. Woodrats have long-term impacts on spatial distribution of soil resources through their persistent middens.

1. Introduction

The distribution patterns of carbon (C) and nitrogen (N) in soils are crucial ecosystem properties, given the importance of these biogeochemical pools to regulating energy and nutrient availability to organisms, modifying soil moisture retention capacity, and ultimately affecting local-to-global biogeochemical cycles (Schlesinger and Bernhardt, 2013). Biogeochemical pools may be affected by ecosystem engineers, organisms that modify environmental conditions and resource pools through non-consumptive activities (Jones et al., 1994). Ecosystem engineers differ greatly in their effects on environmental conditions and resource pools, depending on the behavioral characteristics of the organism, the environment being altered, and the scales of time and space involved (Hastings et al., 2007; Law et al., 2017; Wilby, 2002). Animals that engineer the environment by creating persistent structures have the potential for particularly long-lasting impacts, as environmental modification via structure presence may continue far beyond the lifespan of the responsible ecosystem engineer (Wright et al., 2004). The environmental impact of engineered

structures depends on several factors, including how continuously the structure is used and maintained, post-maintenance longevity, spatial distribution and density of structures, the number of resource flows (e.g., energy, nutrients, water) that are modulated, and the persistence of ecological effects after the engineer's active modifications cease (Jones et al., 1994; Wilby, 2002). An improved understanding of the temporal and spatial impacts of engineered structures is an important component to improving knowledge of ecosystem engineering impacts on biogeochemical pools and processes (Hastings et al., 2007; Levin, 1992).

The temporal and spatial dynamics of ecosystem engineering may be particularly important in environments characterized by spatial heterogeneity in resources. For example, fertile resource islands from woody plants are key structural components of dryland ecosystems. These patches of high soil resource availability, which are derived largely from plant modification of organic matter inputs and accumulation, provide critical resources for autotrophs and heterotrophs (Garcia-Moya and McKell, 1970; Schlesinger and Pilmanis, 1998). Plants further reinforce fertile resource islands through modifying the

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environmental conditions that control litter decomposition and soil respiration, key biogeochemical processes affecting soil C and N pools (e.g., Barron-Gafford et al., 2011; Hibbard et al., 2001; Throop and Archer, 2007). However, animals in these systems can also play key roles in modifying resource distribution, with animals altering local patterns of plant community composition, primary productivity, and soil resource pools as direct and indirect consequences of consumptive activities (Eldridge et al., 2012; Heske et al., 1993; Kerley et al., 1997; Smith and Throop, 2018). Ecosystem engineers in these systems can leave persistent structures that modify biogeochemical pools and local biodiversity (Whitford and Steinberger, 2010; Zak and Whitford, 1988). These structures have the potential for considerable impact on dryland ecosystems, but the temporal impacts of engineered structures on soil biogeochemical pools and processes are not well understood.

Woodrats (*Neotoma* spp.) are structure-building ecosystem engineers that are common in many western North American drylands. Two woodrat species, *Neotoma micropus* and *N. albigula*, inhabit the Chihuahuan Desert (northern Mexico to west Texas and southern New Mexico, USA) where they may be important contributors to biogeochemical heterogeneity through ecosystem engineering (Whitford and Steinberger, 2010). Woodrats construct above-ground stick nests (hereafter termed ‘middens’) with material obtained within their home ranges (usually within a 50 m radius of the midden; Vaughan, 1990). This material consists primarily of sticks and other plant parts, rocks, and supplemental materials such as bones and animal excreta if available (Vaughan, 1990). Woodrat middens may make important contributions to spatial heterogeneity of biogeochemical pools through concentrating considerable portions of the available woody debris (e.g., wood in middens accounted for 7–42% of standing dead and surface wood in the Chihuahuan and Sonoran Deserts; Zak and Whitford, 1988). Middens alter the microclimate and are hotspots for decomposer organisms, leading to potential sinks for woody decay (Zak and Whitford, 1988). The large amount of organic matter accumulation, along with woodrat urine and feces inputs, suggests that middens are biogeochemical resource islands. Indeed, interest by Greene and Reynard (1932) in finding alternative sources of commercially-viable available N led them to compare soil N derived from woodrat middens to that of bare patches and kangaroo rat burrows. Soils below middens had higher concentrations of nitrate (NO_3^-) than kangaroo rat burrows or bare soil (Greene and Reynard, 1932). More recently, soil directly beneath active middens was found to have higher concentrations of soil organic matter and greater N mineralization rates compared with bare soil patches (Zak and Whitford, 1988; Whitford and Steinberger, 2010).

Woodrat middens can be persistent structures in landscapes, with successive woodrat occupants maintaining a single structure far beyond the lifespan of the original occupant. At an extreme, woodrat midden occupation for thousands of years has been documented in protected environments (Betancourt et al., 1990). However, midden turnover is more rapid in lowland desert environments where middens are typically located under shrubs (Olsen, 1973). Middens are occupied by a single woodrat, although unoccupied middens are common (H. Campos, pers. obs.), perhaps as a result of high fluctuations in desert rodent populations. These unoccupied middens (hereafter ‘decayed middens’) can persist in the landscape for many years (Olsen, 1973), although they exhibit visible decay following cessation in inputs of fecal material, urine, and additional structural materials. It is unknown whether modification of soil C and N pools underneath middens responds to midden abandonment and decay. Furthermore, mechanisms for midden impacts on soils are poorly understood; middens may have long-term impacts on soil biogeochemical pools if they mediate litter decomposition and subsequent inputs to soils and this may change with midden activity status.

Here, we investigated the role of active and decayed *Neotoma* middens on biogeochemical pools and processes in the northern Chihuahuan Desert. Specifically, we asked 1) how are soil organic carbon (SOC), total nitrogen (N), extractable nitrogen (NH_4^+ and

NO_3^-), and soil moisture affected by the presence and condition of middens above the soil surface and 2) how are litter decomposition dynamics affected by the presence and condition of middens? We hypothesized that shrub patches with woodrat middens would increase soil nitrogen, SOC, soil moisture, and decomposition rates relative to shrub patches without middens and that decaying middens would have intermediate properties between active middens and no midden patches.

2. Methods

2.1. Study design

This study was conducted in the Chihuahuan Desert Rangeland Research Center, 24 km north of Las Cruces, New Mexico, USA. The study area was located along the eastern-facing alluvial fans of Mt. Summerford in the Doña Ana Mountains (32.500° , -106.791°). The climate is arid, with a mean (SE) annual temperature of $14.7 \pm 0.58^\circ\text{C}$ and mean annual precipitation of 245.1 ± 85 mm. Most of the annual precipitation occurs as summer monsoons from July to September (Wainwright, 2006). Precipitation was above average during our study period (332 mm for 20 June 2014–19 June 2015). The seasonal precipitation distribution was relatively typical, with 201 mm falling during the summer monsoons. Soils in the study area are gravelly sandy loam Typic Haplocalcids of the Nickel-Upton association within an alluvial fan and ridge landform setting (Soil Survey Staff, 2006).

The dominant perennial plants are shrubs; the inter-arroyo ridges are dominated by creosote bush (*Larrea tridentata*) and tar bush (*Flourensia cernua*) whereas the arroyo margins are dominated by honey mesquite (*Prosopis glandulosa*). Banana yucca (*Yucca baccata*; hereafter “*Yucca*”) are common along both the arroyo margins and ridges. *Neotoma* middens are frequently constructed under *Yucca* in this landscape. The structure of *N. micropus* and *N. albigula* middens are not easily distinguished in shrubland habitats such as our study site (Whitford and Steinberger, 2010), so we did not differentiate them for this study.

We identified three different “patch types” to assess midden presence and activity status impacts on biogeochemical pools and processes. All patch types were located below *Yucca* canopies, but they differed in midden presence or activity (Fig. 1). *Yucca* individuals with middens were located by systematic visual searches within the study area. We located 34 middens in this search. We determined that 15 of the middens were currently in use (hereafter called “active midden”; Fig. 1a), as evidenced by a well-maintained dome structure and signs of recent woodrat activity (e.g., fresh droppings in the vicinity of the midden, *Yucca* leaf blades with fresh woodrat herbivory, visible runways leading to entrances, and green litter additions to midden structure). We classified 15 middens as abandoned and decayed to the point of non-utility to woodrats (hereafter termed “decayed midden”; Fig. 1b). The final four middens were discarded for this study because they exhibited evidence that they had recently suffered substantial structural damage, perhaps from *Neotoma* predators. As a control for midden presence, we selected 15 *Yuccas* without middens (hereafter called “no midden”). To understand how *Yucca* presence affected baseline soil chemistry, we also selected 15 shrub intercanopy bare soil areas that were at least 10 m away from *Yucca* or other shrub patches (hereafter called “intercanopy”).

2.2. Soil carbon and nitrogen

We collected soil samples at each of the replicate patches to assess how midden presence and condition affected soil organic carbon (SOC), total nitrogen (N), and seasonally-driven changes in extractable inorganic nitrogen (NO_3^- and NH_4^+) and soil moisture beneath the middens. We collected samples at each of the replicate patches (active midden, decayed midden, no midden) at four times during a six-month

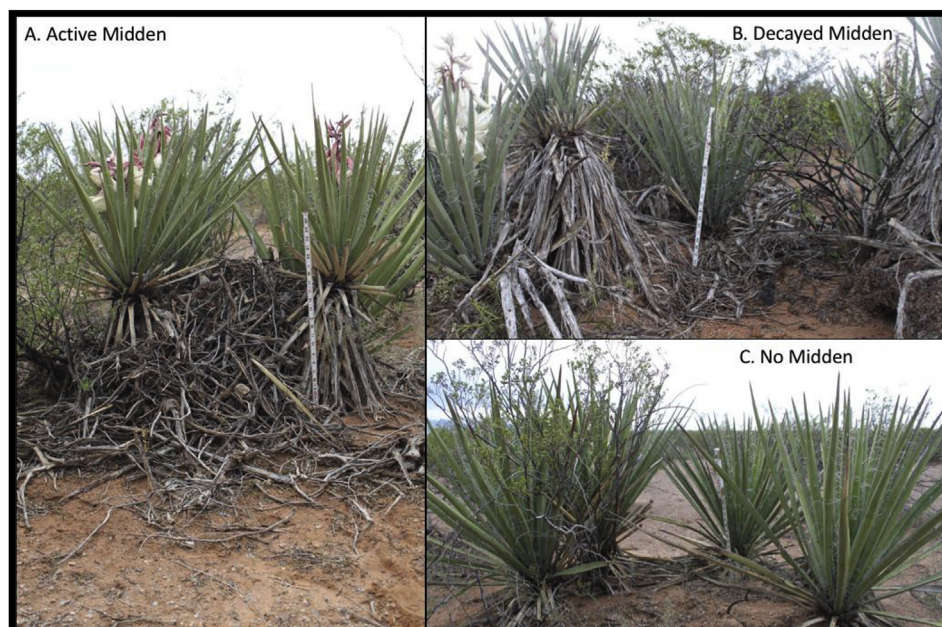


Fig. 1. *Yucca baccata* patches with (a) an active midden present within the patch, containing recent woodrat additions, (b) a decayed midden present within the patch, with midden structure collapsed and in an advanced state of decomposition in which wood litter is highly fragmented, and (c) no midden and no evidence of woodrat activity. The white stick in each photo is 1 m.

period in order to account for seasonal variability in antecedent temperature and moisture conditions (Fig. 2a; 3 July, 24 July, 5 August 2014; 5 January 2015). We collected soil samples using a 2.3 cm diameter soil corer to a depth of 5 cm. Active middens were lifted at the edge using a flat spatula high enough to insert the soil corer perpendicular to the ground. At decayed middens the midden material was moved aside in order to insert the core. At patches with no middens, soil cores were taken within 10 cm of the base of the *Yucca*. *Yucca* litter on the soil surface (dead leaves and caudexes) was removed prior to sampling. To embrace possible spatial variability in soil properties present, we collected two soil cores per patch for every sampling date and combined these two cores. Soils were stored on ice in coolers while in the field and then transferred later in the day to a 4 °C cooler. Soil samples were passed through a 2 mm sieve prior to analysis.

We did not expect seasonal changes in SOC and total N, so we analyzed soil samples for these variables from just one summer sampling date (05 August 2014; lack of seasonal pattern confirmed through analysis of a subset of samples from other dates). We also analyzed soils collected on 30 June 2015 from the bare baseline areas for SOC and total N. For these analyses, a subsample from each sample was dried at 60 °C and ground using a ball mill (8000D, SPEX Certiprep, Metuchen, New Jersey, USA). Prior to analysis, samples were acid fumigated to remove any carbonates present (Harris et al., 2001). Analyses for SOC and total N were conducted using an elemental analyzer (ECS 4010, Costech Analytical Technologies, Valencia, California, USA).

Soil samples from all four sampling dates were analyzed for extractable N. Extractions were conducted on 10 g soil subsamples using 100 ml of 2.0 M potassium chloride (Robertson et al., 1999). The soil-KCl mixture was shaken by hand for 1 min and allowed to settle for 12 h. The solution was filtered using Whatman 3 qualitative filter paper, stored at 4 °C, and analyzed within three weeks of extraction. Spectrophotometric analyses were conducted for NH_4^+ and NO_3^- using a microplate reader (Doane and Horwath, 2003; Rhine et al., 1998). For the NH_4^+ assay, 70 μl sample solution was mixed with 50 μl of citrate, 50 μl of PPS-nitroprusside, and 25 μl of buffered hypochlorite. The plates were incubated for 2 h in the dark at room temperature and read at 660 nm. For the NO_3^- assay, 100 μl of sample solution and 100 μl vanadium (III) chloride reagent were loaded in microplate wells in triplicates. The plates were incubated for 3 h in the dark at room temperature before being read at 540 nm. Samples with high NO_3^- concentration were re-run following dilution if necessary. Soil

gravimetric water content was calculated for 10 g soil subsamples. A wet-dry correction factor was applied to extractable N values using the gravimetric soil moisture content of each sample.

2.3. Litter decomposition

We assessed decomposition rates of leaf and wood substrates in the three patch types using a 12-month litterbag experiment. Honey mesquite (*Prosopis glandulosa*) leaflets and kiln-dried commercial poplar (*Populus* sp.) dowels served as common substrates. Litterbags (8.5 × 8.5 cm) were constructed of fiberglass window screen (20 × 20 mesh, ~0.9 mm openings, Phifer Wire Products, Tuscaloosa, Alabama, USA). We collected mesquite leaflets in November and December 2013 when they were naturally senescing. Leaves were shaken off the branches directly into paper bags and then ‘air dried’ at 30 °C for 2–4 days. We hand-sorted the collected litter, removing rachises, twigs, and leaflets with visible damage (e.g., herbivory or fungus). We filled each litterbag with 2 g of leaflets. In order to establish a wet-dry mass correction factor for mesquite litter, we collected a 2 g litter subsample for every ten litterbags filled, dried the subsample at 60 °C, and reweighed it to obtain dry mass (Throop and Archer, 2007). For the wood litter substrate, we cut poplar dowels (0.32 cm diameter) into 4 cm segments and placed five segments in each litterbag. Use of litterbags for the wood litter helped with relocating the litter in the middens on the collection dates and ensured that the two litter types experienced comparable microclimates. We dried 10% of the dowel segments at 105 °C to obtain a wet-dry correction factor.

We deployed litterbags in the field on 20–25 June 2014, placing 12 litterbags in each of the 45 patches (3 patch types × 15 replicate patches/patch type × 6 collection times × 2 litter substrates = 540 litterbags). At active or decomposed midden patches, bags were lodged under the midden structure and above the soil surface, 2–4 cm from the edge of the midden. The midden was lifted using a flat spatula. At no midden patches, bags were placed under senesced *Yucca* leaves and/or fallen, senesced caudexes. All litterbags were secured in place using sod staples. We collected one replicate litterbag per litter substrate per replicate patch at each of the six collection times (months 0, 1, 2, 3, 6, and 12). We used brushes to manually clean litter of foreign particles (e.g., adhered soil, fungal hyphae, roots), oven dried the litter at 60 °C (leaflets) or 105 °C (dowels) until a stable mass was reached, and measured litter dry mass. While 105 °C is above the temperature at

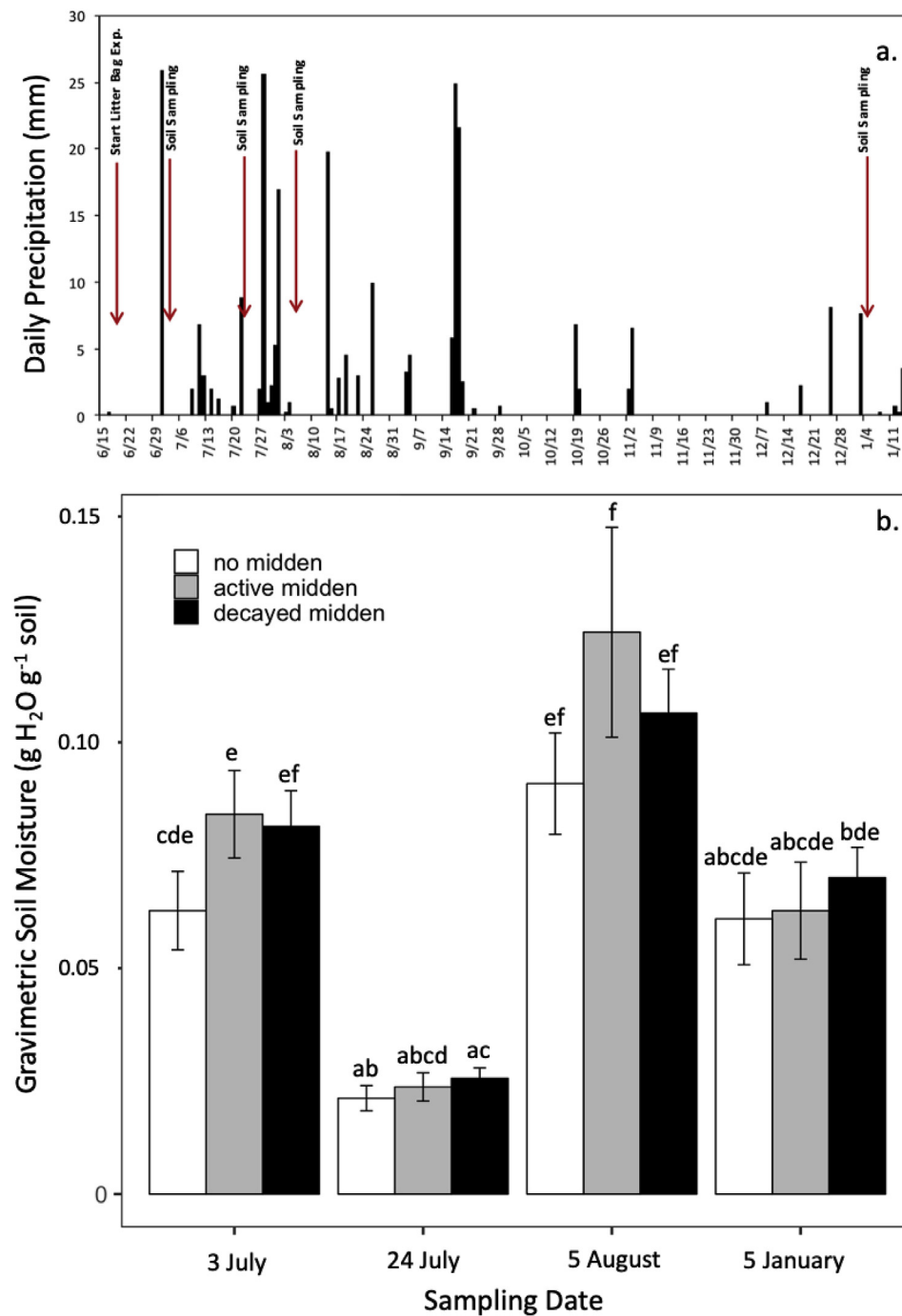


Fig. 2. a) Precipitation events as recorded by Jornada Basin LTER weather station (32.31°, -106.79°) from 15 June 2014–15 January 2015 (data provided by Jornada LTER). Arrows indicate the start of the litter bag experiment and soil sampling dates. b) Mean gravimetric soil moisture from soil cores (0–5 cm) collected on four different dates at *Yucca* patches with no woodrat midden, an active midden, or a decayed midden. Error bars represent $\pm$ SE (N = 15 replicates of each patch type). Bars with the same letters are not significantly different from each other.

which N may volatilize, the higher temperature was necessary to completely dry the wood. As the poplar dowels were kiln dried at temperatures $> 105^{\circ}\text{C}$ during production, our 105°C temperature drying should not have significantly altered wood chemistry. We ground the mesquite leaflet litter into a homogenous mixture for analysis using a ball mill (8000D, SPEX Certiprep, Metuchen, New Jersey, USA). We used a hand-held drill and a 5 mm drill bit to produce sawdust from the wood litter for analyses. To prevent soil accumulation on litter from affecting calculated mass loss, we estimated ash-free mass remaining for each litterbag from mass remaining and percent ash. We determined percent ash from the mass remaining after burning

subsamples from each litterbag in a muffle furnace at 500°C for 5 h. We calculated decay constants for each litter type at each replicate patch using a single exponential decay model ($M_t = M_0 e^{-kt}$; Olson, 1963). In this equation, M_t is the ash-free litter mass at time t , and M_0 is the ash-free initial litter mass, and k is the decay constant. We analyzed triplicate litter samples for C and N content using an elemental analyzer (ECS 4010, Costech Analytical Technologies; Valencia, California, USA).

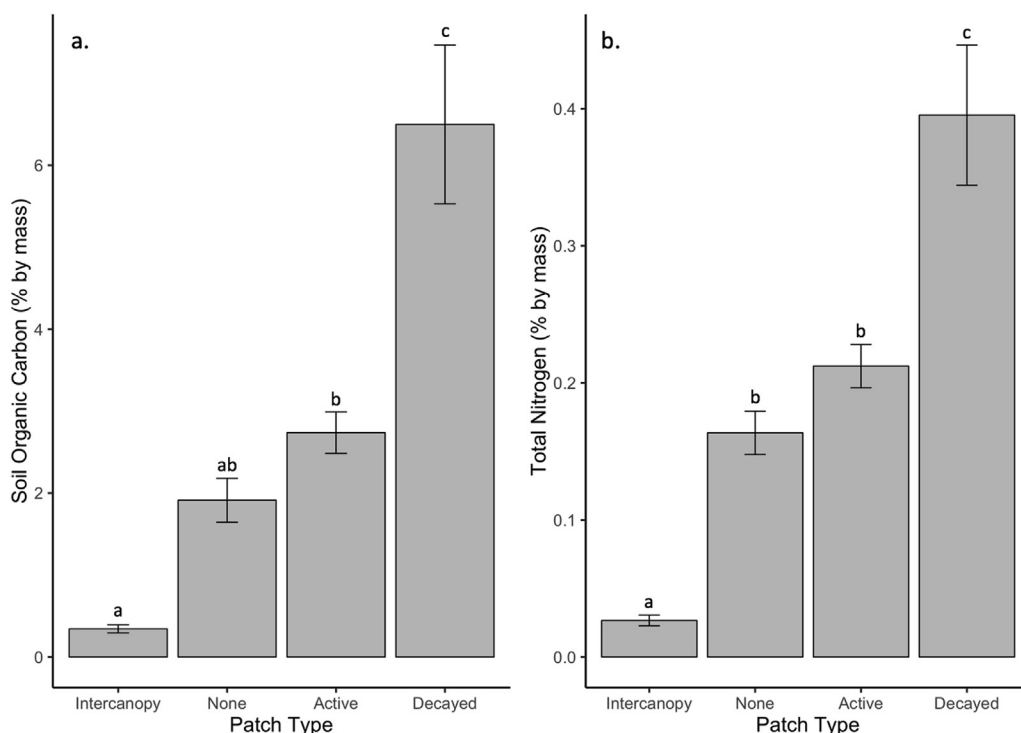


Fig. 3. Mean and standard error for percent a) soil organic carbon and b) total soil nitrogen for intercanopy patches (away from *Yucca* and other shrubs) and *Yucca* patches containing no midden, an active midden or a decayed midden ($N = 12\text{--}15$ replicates per patch type). Error bars represent $\pm$ SE. Bars with the same letters within a panel are not significantly different.

2.4. Statistical analyses

To evaluate how soil organic carbon (SOC), total soil N, and soil C:N ratio differed with patch type, we conducted one-way analysis of variance (ANOVA) procedures using patch type (intercanopy, active midden, decayed midden, no midden) as the main effect. We used a mixed-effects model approach (Bates et al., 2015) to evaluate how nitrate (NO_3^-), ammonium (NH_4^+), and soil moisture differed with patch type and sampling date, with identity of individual patches considered a random effect. We analyzed decomposition data for the two litter substrates separately. We used one-way ANOVAs to assess whether the decay constant, k , differed among patch types. We also assessed differences in litter mass remaining among patch types at the final (12 month) collection time with a one-way ANOVA for each litter substrate. The patch types were not blocked for the analysis as available middens were not spatially co-located appropriately for blocking. Significant ANOVAs were followed up with Tukey's *post-hoc* tests to discern significant pairwise differences. We used $\alpha = 0.05$ for all statistical analyses and transformed the data if needed to conform to the assumptions of ANOVA. We ran analyses using R version 3.5.2 (R Core Team, 2018).

3. Results

3.1. Soil moisture

Mean gravimetric soil moisture content among all midden types ranged from $0.021 \text{ g H}_2\text{O g}^{-1}$ soil on 24 July to $0.124 \text{ g H}_2\text{O g}^{-1}$ soil on 5 August (Fig. 2b). Soil moisture differed with sampling date ($F_{8,126} = 266.63$, $P > 0.0001$), with the highest soil moisture contents coinciding with large rainfall events preceding the sampling dates. Soil moisture did not differ among patch types ($F_{2,42} = 1.19$, $P = 0.31$) and there was no interaction between sampling date and patch type ($F_{6,126} = 0.91$, $P = 0.49$).

3.2. Soil carbon and nitrogen

Soil organic carbon differed among the four patch types

($F_{3,51} = 22.51$, $P < 0.0001$), with greatest SOC in the decayed middens (Fig. 4a). Both active and decayed middens had greater SOC content than intercanopy areas away from *Yuccas* or other shrub patches (Fig. 3a). Similarly, total soil N differed among patch types ($F_{3,52} = 28.46$, $P < 0.0001$), with greater N in the decayed than no midden or active midden patches (Fig. 3b). Nitrogen concentration in intercanopy spaces was lower than any of the midden patch types.

Soil extractable ammonium (NH_4^+) differed among sampling dates ($F_{3,126} = 43.42$, $P < 0.0001$), remaining low for the two dates in July, peaking for the August sampling date, and declining to moderate values for the January sampling date. Soil NH_4^+ differed among patch types (Fig. 4a; $F_{2,42} = 7.75$, $P < 0.005$) and there was a significant interaction between patch type and date ($F_{6,126} = 4.54$, $P < 0.0005$) such that NH_4^+ was enhanced in the decayed midden patches in the August sampling date.

Similar to NH_4^+ , soil extractable nitrate (NO_3^-) differed among dates (Fig. 4b; $F_{3,126} = 30.48$, $P < 0.0001$), with greatest values in the August sampling date. Nitrate also differed among patch types ($F_{2,42} = 44.63$, $P < 0.0001$), with greatest NO_3^- in decayed midden patches and lowest NO_3^- in no midden patches. There was no interaction between patch type and sampling date ($F_{6,126} = 1.64$, $P = 0.14$).

3.3. Litter decomposition

Mesquite litter decayed exponentially, with the majority of the decomposition occurring in the first six months (Fig. 5a). Patch type influenced mesquite litter remaining at the final (12 month) collection time (Fig. 5a; one-way ANOVA, $F_{2,42} = 8.28$, $P < 0.001$), when there was significantly less mesquite litter remaining in litterbags deployed at decayed midden patches than those deployed at no midden or active midden patches. Litter decay constants (k), which integrate decomposition across the entire study period, were similarly enhanced for mesquite litter in decayed midden patches relative to the other two patch types (Table 1; $F_{2,42} = 10.98$, $P < 0.001$).

In contrast to rapid decay mesquite litter decay, poplar dowel decomposition proceeded slowly for the entire 12 months. At the conclusion of the 12 month experiment, there were no among-patch differences in poplar dowel mass (Fig. 5b; one-way ANOVA, $F_{2,39} = 0.191$,

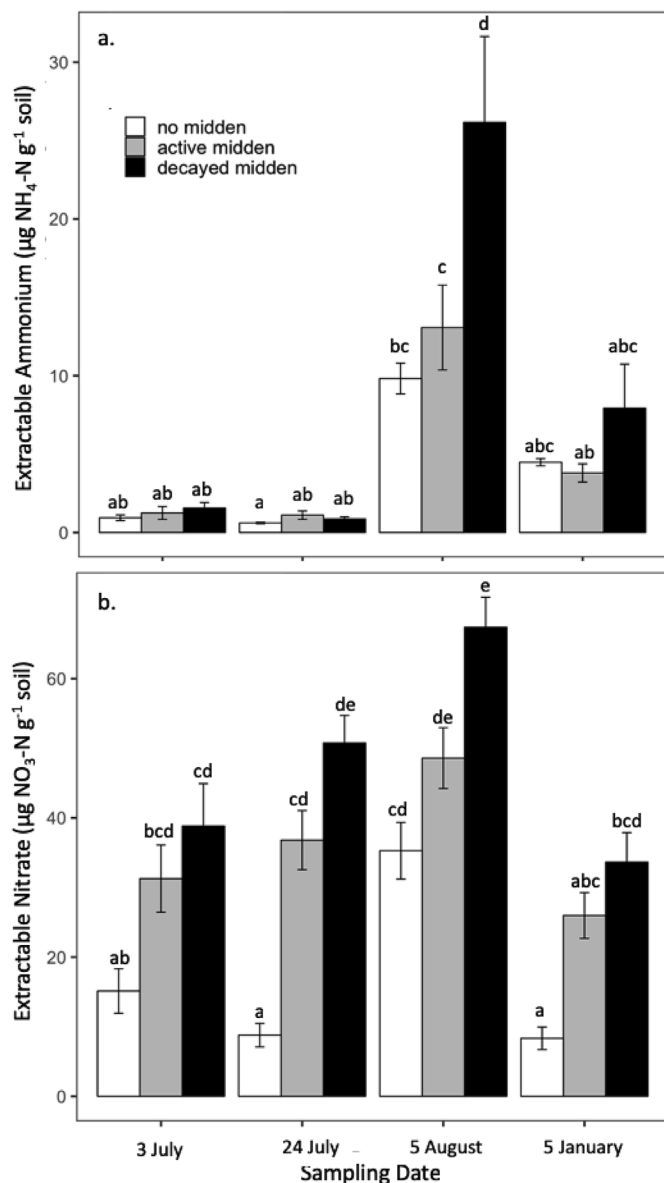


Fig. 4. Soil a) extractable ammonium and b) extractable nitrate in the upper soil layer (0–5 cm) from four different dates at *Yucca* patches with no woodrat midden, an active midden, or a decayed midden. Values are means $\pm$ SE ($N = 15$ replicates per patch type). Within a panel, bars with the same letters do not differ significantly from each other.

$P = 0.83$). The decay constant was lower for active middens than the other two patch types (Table 1).

4. Discussion

The presence and activity status of woodrat middens in *Yucca* patches had direct impacts on key soil biogeochemical pools (SOC, total N, and extractable N) while also impacting leaf litter decomposition, an important biogeochemical process that influences SOC and nutrient availability. These responses suggest important roles of woodrats in modifying local-scale resource availability and indicates that impacts of structures built by these ecosystem engineers can persist well beyond structure abandonment. In fact, the greatest biogeochemical impacts occurred only after structures were no longer maintained, with mesquite litter decomposition, SOC, soil total N, and extractable N enhanced in decaying middens. These data support the idea that not only can the effects imparted by an ecosystem engineer extend beyond the

lifespan of the engineer (Jones et al., 1994; Hastings et al., 2007), but also that some of the greatest effects may be through the degradation of the engineered structure.

4.1. Midden effect on decomposition

Decomposition differed dramatically between the two litter substrates in the one-year study, with mesquite leaflets losing about half their mass and wood dowels losing only a few percent of their mass. Rapid decomposition of mesquite leaflets was expected as this substrate is high in N and typically decays quickly (e.g., Throop and Archer, 2007). Decay coefficients for mesquite ($0.6\text{--}1.0\text{ y}^{-1}$) were in the realm of reported prior measurements for this species at this site, which vary considerably based on precipitation. Prior reported values for a one-year decomposition period were $k = 0.5\text{ y}^{-1}$ and $k = 1.5\text{ y}^{-1}$, during which total precipitation was 115 mm and 366 mm, respectively (Hewins et al., 2013; Hewins and Throop, 2016). Total rainfall during the present study was 332 mm. In contrast to rapid mesquite litter decomposition, poplar dowel decomposition was extremely slow. This difference may be in part due to very low dowel N content. In addition, the wood was kiln dried, which can lead to chemical changes (e.g., loss of nitrogenous compounds, lignin and hemicellulose degradation) and reduced fungal colonization (Candelier et al., 2016). Depressed fungal colonization would be significant as fungi are key decomposers of wood (Boddy and Watkinson, 1995) and may be the primary decomposers in middens (Anders, 1992). While we expected faster decomposition for mesquite leaflets than wood, we also expected that specialized communities for wood decay in middens would lead to greater wood decay rates in patches with middens than in no midden patches. Slow fungal colonization may account for some of the decomposition differences; at decayed middens there was on average only 1% woody mass loss during the initial 0–6 month period while this increased five-fold during the 6–12 month period. White rot fungus was visually apparent on dowels from all patch types only at the 12-month collection (H. Campos, pers. observation). Given the slow start to wood decomposition, a longer study period is necessary to more fully assess if there are among-patch differences in decay rates. Given the minimal differences in wood decay among patch types, we focus the rest of our decomposition discussion on mesquite litter decay.

Mesquite litter decomposition differences among *Yucca* patch types suggests that biophysical factors affected by midden presence and activity state influence decomposition processes. We anticipated that microclimate differences among patch types might drive decomposition differences, but we did not detect among-patch differences in soil moisture (Fig. 2b). However, these soil measurements were taken opportunistically with soil core collection; such infrequent measurements may fail to detect microclimate patterns that would emerge with more frequent measurements. We also do not know how these soil moisture measurements taken from soil underneath the middens would relate to conditions above the soil surface, where litterbags were placed. However, a prior study found increased relative humidity and decreased temperature inside middens on a warm summer day relative to exterior conditions (Whitford and Steinberger, 2010). Similarly, high microbial communities and decomposition in muskrat (*Ondatra zibethicus*) mounds were attributed to insulating properties of the mounds (Wainscott et al., 1990). Microclimate modifications by woodrat middens, if present, are likely to enhance the proportion of time that conditions are suitable for microbial activity, thus enhancing decay rates (Joly et al., 2017). Given this possibility, it was surprising that decomposition was substantially elevated only in decayed middens and not in active middens.

Structural differences between active and decayed middens may contribute to differences in decomposition rates between these patch types. Decayed middens are flat, fragmented, and darker on the surface than active middens. It may be that these structural differences affect microclimate, perhaps increasing heat absorption of decayed mounds

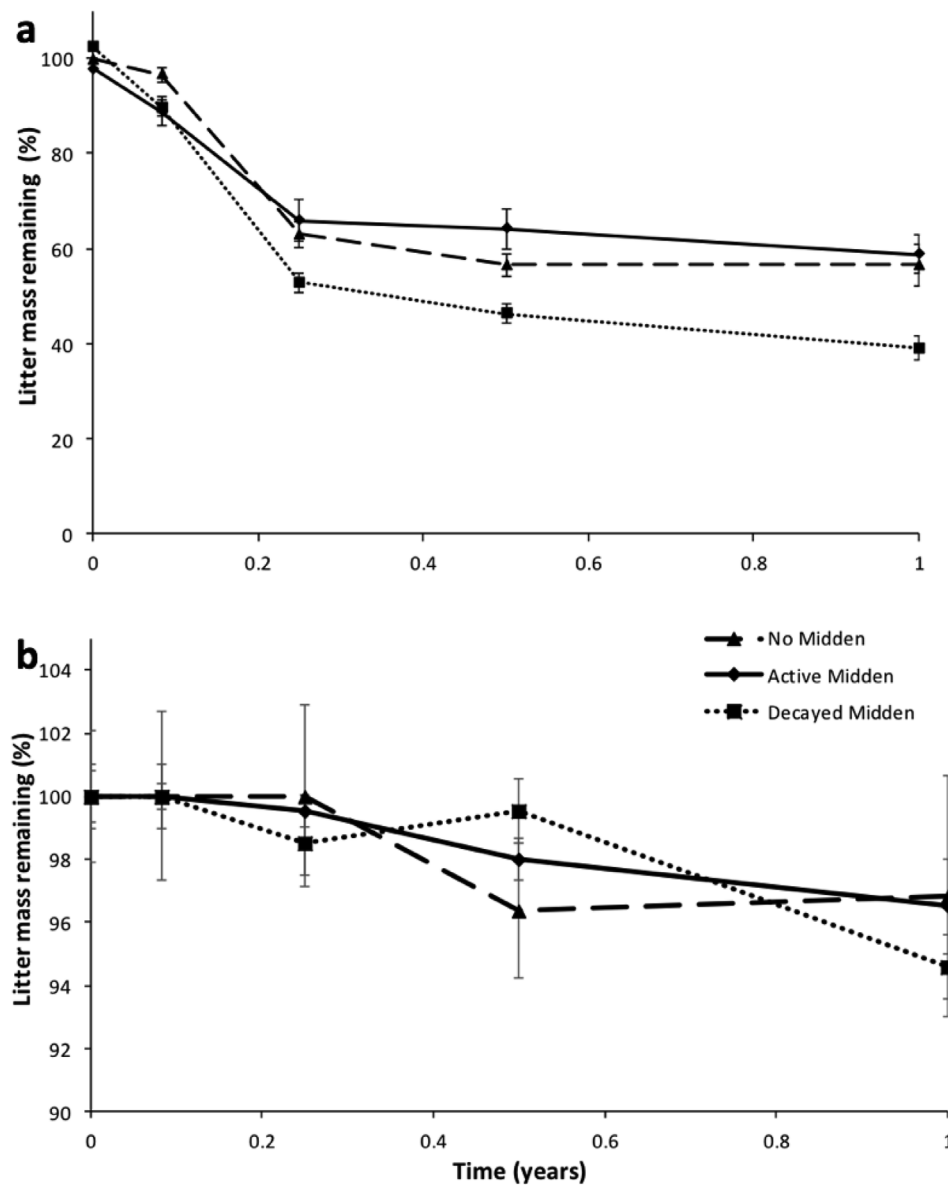


Fig. 5. Ash-free mass remaining of a) mesquite (*Prosopis glandulosa*) leaf litter and b) poplar wood dowels (*Populus* sp.) in litterbags recovered at *Yucca* patches 0, 1, 3, 6 and 12 months after being placed in the field. Values are means $\pm$ SE (N = 13–15 litterbags per patch type at each collection time, depending on litterbag recovery). Note the difference in y-axis scales for the two litter types.

Table 1

Litter decay constants for mesquite leaflets and poplar dowels after one year of exposure in different *Yucca* patch types. A decay constant was calculated for each replicate patch; values are means and standard error k values of all the replicate patches (N = 13–15 replicate patches per patch type, depending on litterbag recovery rate). Within a litter type, decay constants do not differ for patch types with the same superscript.

Yucca Patch Type	Decay Constant (k , y^{-1})	
	Mesquite leaflets	Poplar dowels
No Middens	0.61 ± 0.068^a	0.10 ± 0.026^a
Active Middens	0.54 ± 0.077^a	0.03 ± 0.005^b
Decayed Middens	1.00 ± 0.079^b	0.05 ± 0.014^{ab}

relative to active mounds. The flattened structure of decayed middens may also reduce airflow, potentially decreasing evaporative losses and increasing relative humidity. Detailed microclimate studies are needed to assess these differences and confirm if they contribute to observed

higher decomposition in decaying middens.

4.2. Midden effects on soil carbon and nutrient pools

Concentrations of SOC and N in surface soils below middens were positively affected by *Yucca* and further enhanced by woodrat middens. The substantial increase in SOC and total soil N in no-midden *Yucca* patches relative to intercanopy baseline locations was consistent with the well-documented islands of fertility phenomenon in dryland ecosystems. Specifically, SOC and nutrients accumulate in shrub subcanopies as a result of shrub-derived organic inputs, enhanced animal activity in subcanopy locations, or entrapment of wind- and water-transported material (Archer et al., 2017; Garcia-Moya and McKell, 1970). While we expected a *Yucca* influence on soil pools, it was larger than we anticipated given the small size of *Yucca* and their presumably minimal impact on the subcanopy microclimate due to their tall stature and limited canopy cover. Furthermore, *Yuccas* tend to retain their leaves following senescence unless they are removed by woodrats (Smith and Throop, 2018), minimizing aboveground litter inputs.

Enhanced SOC under active middens relative to no midden *Yucca* patches suggests that SOC accumulates with inputs from middens over time, although SOC and total N increases under middens were significantly greater than no midden patches only for decaying middens. In contrast, Whitford and Steinberger (2010) reported significant enhancement in SOC under active middens. However, this discrepancy seems to be a function of sampling design; Whitford and Steinberger's no-midden samples were collected 3 m away from active middens, but were not necessarily under shrubs.

We had expected that SOC and soil N would be elevated in decaying middens, but were surprised that pools were so much greater in decaying middens than active middens. Why might decaying middens have so much higher SOC and N pools? One possibility is that there is limited decay of structural materials in active middens relative to decaying middens, limiting transfer of C and nutrients from the midden into soil pools through leaching or physical movement of fragmented material. The stick-dominated midden construction at our study site may limit leaching or fragmentation due to slow woody decay rates; wood decay is particularly slow when it is not in contact with the soil (van der Wal et al., 2007). Active maintenance of middens by woodrat inhabitants could counteract woody decomposition, with midden structural integrity maintained by limiting contact of woody material with the soil or removal and replacement of decaying material that begins to fragment. Alternatively, it may be that soil disturbance by woodrats limits SOC accumulation in active middens, similar to tillage impacts in agricultural soils (Six et al., 2002).

Soil extractable N followed the same general patterns as SOC and total N, with decayed middens typically have highest extractable N. However, there were also strong temporal patterns, where nitrate and ammonium were much higher at warm and moist sampling dates than dry or cooler sampling dates. This finding reflects typical moisture and temperature limitation of microbial N transformations in drylands (Collins et al., 2008). The fragmented wood litter in decayed middens likely serves as an important C source for fungi, which may introduce N into these patches from exogenous sources (Boddy and Watkinson, 1995).

4.3. Woodrats as ecosystem engineers

The positive effects on decomposition caused by an engineer-altered environment observed in this study are similar to those reported for beaver lodges (*Castor canadensis*; Naiman et al., 1988; Correll et al., 2000; Law et al., 2017) and muskrat mounds (*Ondatra zibethicus*; Wainscott et al., 1990). Altered biogeochemical pools and processes in found in decaying middens joins evidence from other ecosystems engineers in suggesting that engineered structures may leave legacies on the landscape following abandonment. Studies on abandoned beaver lodges indicate long-term alterations of soil pools and litter decomposition (Correll et al., 2000; Naiman et al., 1988), similar to our findings from woodrat middens. Dostál et al. (2005) found that abandoned ant mounds may not revert to pre-engineered conditions until decades after abandonment. Likewise, disturbances to the soil through biopedturbation may persist following abandonment, such as occurs following recovery from pits dug by American badgers (Eldridge and Whitford, 2009). This present study of three possible *Yucca* patch and woodrat midden activity states suggests a dynamic change in biogeochemical processes through time. *Yucca* and woodrat middens change decomposition dynamics within middens, altering soil resources below middens through time. These changes are enhanced following midden abandonment, ultimately leading to enhanced spatial resource heterogeneity of this arid landscape. A limitation of our study is that we do not know middens ages or the length of time since abandonment. A clearer understanding of the temporal aspects of midden use and abandonment would be important for assessing rates by which woodrat midden modify ecosystem processes.

We found that woodrat middens can alter biogeochemical pools and

processes, but that the greatest impacts occur after middens are no longer maintained. The differential influence of active and decayed middens highlights the importance of assessing not only how engineered structures affect biogeochemical pools and processes, but also how these impacts change throughout the life cycle of the engineered structures. Ultimately, woodrats in the Chihuahuan Desert cause long-term changes in soil biogeochemical pools and processes and these changes persist after structure maintenance has ceased. In this capacity, woodrats alter the spatial patterns of soil C and N, thus enhancing resource heterogeneity in a dryland ecosystem.

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