

Ancient experiments: forest biodiversity and soil nutrients enhanced by Native American middens

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Abstract The legacy of ancient human practices can affect the diversity and structure of modern ecosystems. Here, we examined how prehistoric refuse dumps (“middens”) impacted soil chemistry and plant community composition in forests along the Chesapeake Bay by collecting vegetational and soil nutrient data. The centuries- to millennia-old shell middens had elevated soil nutrients compared to adjacent sites, greater vegetative cover, especially of herb and grass species, and higher species richness. Not only are middens important archaeological resources, they also offer a remarkable opportunity to test ecological hypotheses about nutrient addition over very long time scales. We found no evidence, for example, that elevated nutrients enhanced invasion by non-native species as predicted by the fluctuating resource

hypothesis. However, we did find that elevated nutrients shifted community structure from woody species to herbaceous species, as predicted by the structural carbon-nutrient hypothesis. These results highlight the long-lasting effects that humans can have on abiotic and biotic properties of the natural environment, and suggest the potential for modern patterns of species’ distributions and abundances to reflect ancient human activities.

Keywords Land-use legacies · Shell middens · *Crassostrea virginica* · Forest diversity · Invasion · Nutrient addition · Calcium · Chesapeake Bay, Maryland, USA

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Introduction

A fundamental goal of ecology is to explain variation in the abundance, diversity, and distribution of species across the landscape, and to document how these patterns are altered by human actions. It has been well established that modern humans are radically altering the environment via activities such as deforestation, urbanization, and the widespread exchange of organisms among previously isolated landmasses (Vitousek 1997). At local scales, modern humans may increase species richness due to the introduction of non-native organisms (Sax et al. 2002; Marks et al. 2008; Vellend et al. 2013), but the overall consequences for biodiversity are generally negative (Pimm et al. 1995).

Although less studied than modern human activities, practices predating the Industrial Revolutions can also have lasting impacts on contemporary patterns of species distribution and diversity. For example, the signature of ancient Maya forest gardens remains evident in the composition of modern Belizean forests (Ross 2011), and in Northern France the intensity of Roman agriculture still influences species richness and the composition of forests that have not been farmed for nearly 2,000 years (Dupouey et al. 2002).

Similar legacy effects occur in the United States, often associated with ancient Native American shell middens (Brown 1936; Brennan 1974; Norman 1976; Kelly 2006; Erlandson 2014; Thompson et al. 2013). These middens are refuse dumps of shell and bone from prehistoric peoples and are commonly found along coastal landscapes. They have long-captivated naturalists and archaeologists due to the unique ecological assemblages and cultural materials found there. As early as 1879, naturalists found Florida middens “to be as marked in botanical as in geological features and as regards entomology, incomparable” (Curtiss 1879). Multiple floristic surveys of middens have observed that these sites are species-rich and home to rare species (Brown 1936; Brennan 1974; Norman 1976; Kelly 2006), including one previous assessment of plants on shell middens in the Chesapeake region (McAvoy and Harrison 2012). However, only two studies have paired middens with control sites to rigorously test the hypothesis that middens possess uniquely different ecological communities (Karalius and Alpert 2010; Vanderplank et al. 2014). Karalius and Alpert (2010) examined middens in coastal prairie and scrub communities in central California, and observed that introduced species were more abundant on middens compared to adjacent areas, potentially as a result of the elevated nitrogen levels found on middens. Vanderplank et al. (2014) examined two midden complexes in Baja California and found that one midden complex hosted higher native biodiversity than adjacent sites, but not the other.

Pairing midden sites with adjacent non-midden sites not only permits a rigorous characterization of midden communities, but also provides a unique opportunity to test hypotheses about the ecological effects of nutrient enrichment over time scales rarely seen in the ecological literature. The refuse deposited by ancient peoples in shell middens, for example, has

been shown to significantly enhance soil nutrients, especially N, Ca, P, and Mg, and increase soil alkalinity (Karalius and Alpert 2010; Resende Correa et al. 2011). Compared to the Parks Grass Experiment, a nutrient addition experiment begun in 1856 and described as the “the oldest ecological experiment in existence” (Tilman et al. 1994; Silvertown et al. 2006), these Native American shell middens represent centuries- to millennia-long experimental tests (albeit unintentional) of the outcomes of nutrient enrichment on plant community structure.

Here, we present the first study linking ancient Native American land-use on the Chesapeake Bay to variation in soil traits and plant community structure. In addition, we used these midden communities to examine two ecological hypotheses: the fluctuating resources hypothesis (Davis et al. 2000) and the structural carbon-nutrient balance hypothesis (Graves et al. 2006). The fluctuating resources hypothesis posits that communities become more invisable when there is an excess of unused nutrients (due to disturbance or eutrophication, for example), and predicts that middens should have more non-native species than paired off-midden sites. The structural carbon-nutrient balance hypothesis argues that herbaceous plants should be favored over woody species in low-light, high-nutrient forest environments, primarily because herbaceous species can grow faster but typically require more nutrients per unit biomass to annually replace tissue. Thus we tested the four hypotheses that midden sites would have (1) elevated nutrients, (2) different plant communities, (3) relatively more non-native species, and (4) more herbaceous species than adjacent control sites.

Materials and methods

Site selection

We conducted all research at the Smithsonian Environmental Research Center (SERC; Edgewater, MD; 38°53'N, 76°33'W) on land along the Rhode River within the Chesapeake Bay watershed. SERC and surrounding areas were occupied by Native Americans for over 13,000 calendar years prior to colonial settlement (Gallivan 2011; Rick et al. 2014). During the Woodland period about 3,200–400 years ago, Native Americans intensively harvested eastern



Fig. 1 Photograph of 18AN1323, a typical midden from our study. *Image on the left* shows the site area, including oysters eroded in the high tide line, intact deposits being excavated and

surrounding vegetation. *Image on right* is a closeup of the midden deposits, showing dense concentration of oysters. The image is adapted from Rick et al. (2014)

oysters (*Crassostrea virginica*), as well as other shellfish and vertebrate fauna. The remnants of these harvests are concentrated in shell middens along the shoreline (Fig. 1) and ~50 shell middens have been recorded in the region surrounding SERC (Wright 1973; Gibb and Hines 1997; Cox 2007; Rick et al. 2014).

Beginning in the mid-1600s, the mainly contiguous forests in this area were cleared to support colonial-era tobacco plantations. Soil-depleting tobacco gave way to wheat and grain production in the mid-1800s, followed by dairy farming in the early 1900s. Less is known about Native American land use prior to the mid-1600s, but Native people were practicing horticulture, fishing and collecting shellfish, and probably periodically burning portions of the landscape (Miller 2001). Starting in the early 1960s, SERC began operating as a field research station, with most of the croplands reverting to forest. Thus, the shell middens are currently dispersed throughout a landscape of secondary, coastal plain forests.

In 2011, we identified ten midden sites situated within established secondary forests (Table A1). All are located on dry land adjacent to the Rhode River and its tributaries, but one site (AN1323) has a portion that is partially inundated at high tide. We clearly delineated the boundaries of each midden by examining soil color (midden soils are often darker) and especially by searching for shells and artifacts in eroding exposures and in small (10 cm diameter)

auger holes that we excavated to determine subsurface depths and densities. Each midden was paired with an equivalently sized control site located off the midden, with the same slope, elevation, and aspect as the midden. All control sites were within 5–10 m of the midden to reduce environmental variation between midden and off-midden sites.

Midden deposits were mostly at the soil surface except for 18AN287, which had deposits ranging from ~10 to 40 cm below the surface. All deposits were between ~10 and 70 cm thick and contained dense concentrations of eastern oysters and smaller amounts of other shellfish [*Tagelus plebeius* (stout razor clam), miscellaneous barnacles, *Crepidula* sp. (slipper shells), *Mercenaria mercenaria* (hard-clam), and other small estuarine gastropods], animal bones, pottery fragments, and chipped stone similar to other Chesapeake Bay shell middens (Gibb and Hines 1997). The ten middens ranged from 5 to 126 m² and were separated from each other by at least 1 km, except for four sites (AN308A/B and AN741A/B; Table A1). For these latter sites, we subdivided the shell middens into two separate sites (A and B), because of >10 m breaks in the deposits and changes in topography.

Radiocarbon dating

To determine the age of each midden, we radiocarbon-dated *C. virginica* shells following dating and

calibration procedures provided in Rick et al. (2012). We obtained accelerator mass spectrometry (AMS) radiocarbon dates from individual *C. virginica* shells because this species comprised over ninety percent of the shell fragments and are a reliable material for radiocarbon dating (Rick et al. 2012). The National Ocean Sciences AMS Laboratory at Woods Hole Oceanographic Institute analyzed all radiocarbon samples. We corrected radiocarbon dates for the local reservoir effect using a standard subregional correction ($\Delta R = 118 \pm 21$; Rick et al. 2014) and calibrated them using OxCal 4.2 (Bronk Ramsey 2009, 2013). All ages presented herein are calibrated ages before present (cal BP). For additional information, Rick et al. (2014) recently presented a chronology for 31 shell middens in the Rhode River region, including all of the sites reported here.

Soil measurements

To characterize soil nutrients in both the midden and off-midden sites, we removed the topsoil, and took a core 20 cm deep and 8 cm in diameter from the thickest part of the midden (or an analogous area from off-midden sites). We sent soil samples ($N = 10$ midden samples, 10 off-midden samples) to the Soil and Plant Tissue Testing Lab at the University of Massachusetts at Amherst for analysis. Soils analysis followed standard analytical protocols for evaluating a range of soil nutrients with details available at <http://soiltest.umass.edu/>. This analysis included measurements of a suite of soil properties, including nitrate concentration, pH, extractable macro- and micronutrients (e.g., P, K, Ca, Mg, Fe, S, Al), cation exchange capacity, and percent soil organic matter (loss on ignition) (Table A2).

Plant measurements

We estimated the richness and percent cover (nearest 1 % at ≤ 1 m height above the ground) of all vascular plant species growing in one to seven 1-m² quadrats distributed along transects spanning the longest and widest points of each midden and paired off-midden site ($N = 42$ on-midden and 43 off-midden quadrats). We also measured the diameter at breast height (dbh) of all adult trees. We identified all plants to species (Table A3), and used the USDA Plants Database (plants.usda.gov) to classify the species by origin

(non-native or native) and morphotype (woody species, forb, or graminoid).

Analyses

All analyses were conducted in R (R Foundation for Statistical Computing, version 3.0.1). For analyses of plant community structure, we always included midden as the main effect (on vs. off) and quadrat nested within site as a random factor. We used mixed-effects binomial logistic regression (*glmer* in *lme4* package by Bates, Maechler and Bolker) to analyze differences in percent cover and in the proportion and cover of natives versus non-natives (Warton and Hui 2011). We used a mixed effects linear model (*lmer* in *lme4*) to analyze tree dbh, ln-transforming the data to improve the normality of the residuals. We used a mixed-effects generalized linear model (*glmer* in *lme4*) with a poisson distribution to analyze richness. For all of these models we determined the significance of the fixed effect by comparing the likelihood of nested models with and without midden as a factor. For soil chemistry analyses, we included midden (on vs. off) as a main effect and analyzed the data using *t* tests (*t.test* in the base package *stats*, which assumes unequal variance among samples and applies the Welch df approximation). Because we collected one composite soil sample per midden or off-midden site, we did not include site as a random factor.

Results

Radiocarbon dating shows that two of the shell midden sites (AN308A/B) are up to 3,250 years old (1250–800 cal BC, Table A1). Five sites (AN226, 287, 294, and 741A/B) date to the Late Woodland Period (cal AD 1270–1520). One site (AN296) appears to have formed in the seventeenth century and two sites (AN854 and 1323) date from the early nineteenth century (see Rick et al. 2014). These latter three sites may have been used until the middle of the twentieth century. Thus, shell-based nutrient amendments to these soils have occurred on the order of centuries to millennia.

The shell deposits dramatically enriched the soil (Fig. 2; Table A2). Cation exchange capacity, an integrative measure of soil fertility, was higher in midden soils ($t = -3.7$, $p = 0.008$). Individual

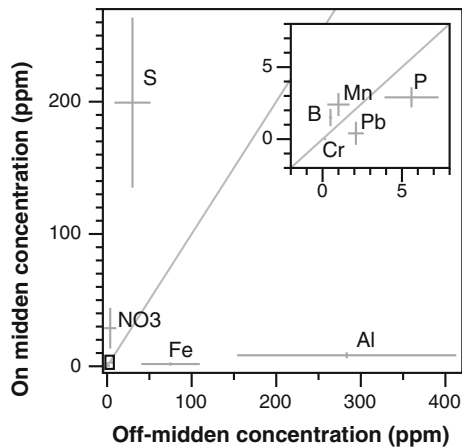


Fig. 2 Concentrations (ppm) of macro- and micronutrients in midden soils versus off-midden soils (mean \pm SEM), with diagonal 1:1 line. Only compounds that significantly differ between soil types are shown (Table A2). Nutrients above the 1:1 line are higher in midden soils and those below the 1:1 line are higher in off-midden soils. The inset figure highlights details from the bottom left of the graph

nutrients were also elevated, especially calcium and nitrate concentrations. Midden soils had almost 45 times more calcium than off-midden soils ($t = -3.6$, $p = 0.011$) and 6.7 times higher nitrate concentrations ($t = -2.8$, $p = 0.020$). Because of the enhanced calcium levels, midden soils had more neutral pH ($t = -15.8$, $p = 0.001$; 7.4 ± 0.2 vs. 4.4 ± 0.3 ; mean \pm 95 % CI). Midden soils also had significantly greater concentrations of boron ($t = -3.2$, $p = 0.016$), manganese ($t = -2.7$, $p = 0.020$), and sulfur ($t = -4.8$, $p = 0.006$), whereas off-midden sites had significantly greater concentrations of chromium ($t = 4.6$, $p = 0.006$), lead ($t = 3.4$, $p = 0.006$), phosphorus ($t = 2.9$, $p = 0.020$), iron ($t = 4.1$, $p = 0.006$), and aluminum ($t = 4.1$, $p = 0.006$). There was no difference in percent organic matter ($t < 0.1$, $p = 0.938$).

Middens had slightly more vegetative cover than adjacent off-midden sites ($\chi^2 = 6.4$, $p = 0.011$); however they had a dramatically different ratio of woody to herbaceous cover (Fig. 3a). Off-midden sites had greater woody cover than did middens (38 % off-middens vs. 26 % on middens; $\chi^2 = 190.4$, $p < 0.0001$; Fig. 3a) and those trees growing on off-midden sites had 128 % larger diameters (16.9 cm dbh off-middens vs. 7.4 cm dbh on-middens; $\chi^2 = 23.4$, $p < 0.001$). In contrast, the vegetation on middens was

composed primarily of forbs and grasses. While middens had 13 % forb cover on average, off-middens had less than 1 % forb cover ($\chi^2 = 703.2$, $p < 0.0001$). Middens also had 57 % greater grass cover than off-middens (26 % on middens vs. 16 % off-middens; $\chi^2 = 208.1$, $p < 0.0001$).

Ancient nutrient amendments also enhanced forest biodiversity, with middens supporting moderately more species on average than off-midden sites ($\chi^2 = 7.3$, $p = 0.006$; Fig. 3b). In addition, middens were more likely to host unique species assemblages. While most of the 92 species identified (58 %) occurred in both midden and off-midden soils, we found 29 species (31 %) exclusively on middens compared to nine species found only off middens (Table A3). Middens had significantly more forb species ($\chi^2 = 15.7$, $p < 0.0001$) and grass species ($\chi^2 = 9.7$, $p = 0.001$), but there was no difference in woody species richness between middens and off-middens ($\chi^2 < 0.1$, $p = 0.923$).

Most of the observed species (81 %) were native, and both the richness of natives ($\chi^2 = 3.9$, $p = 0.04$; Fig. 3b) and non-natives ($\chi^2 = 5.3$, $p = 0.021$; Fig. 3b) were higher on middens than off middens. However, the relative number of native versus non-natives species did not change between midden and control sites ($\chi^2 = 1.1$, $p = 0.278$) and the relative proportion of native versus non-native cover was higher on middens than off middens ($\chi^2 = 120.5$, $p < 0.0001$). Thus, contrary to the prediction that nutrient enrichments would shift plant composition towards non-native species, we found that plant communities on middens were more likely to be comprised of natives.

Discussion

Archaeological refuse dumps represent replicated, albeit unintentional, experiments that can be used to test ecological hypotheses over long time frames. We used middens to examine both the structural carbon-nutrient balance hypothesis (Graves et al. 2006) and the fluctuating resource hypothesis (Davis et al. 2000). Consistent with the first hypothesis we found that elevated nutrients on midden soils coincided with a shift from primarily woody to herbaceous plants. Contrary to the latter hypothesis, we found that non-natives were not more common on high-nutrient

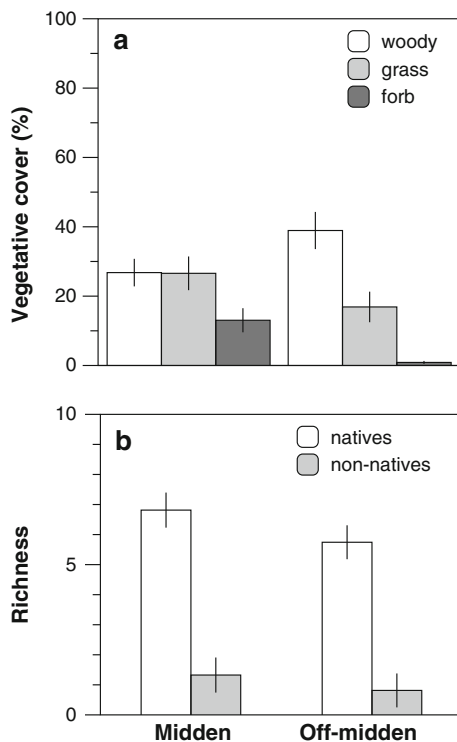


Fig. 3 Plant community structure on and off-middens with **a** vegetative cover (mean \pm SEM) and **b** richness of natives and non-natives shown (mean \pm SEM for overall richness)

middens. More generally, we found that ancient human activities shifted community structure and enhanced forest diversity at the landscape-scale, and that these effects persisted for thousands of years.

Shell and other midden soils around the world often have unique nutrient composition, and are significantly enriched compared to surrounding areas. Resende Correa et al. (2011) recently documented significantly elevated levels of calcium, phosphorus, and other nutrients in Brazilian shell middens, but it remains to be seen how these may have influenced plant communities. Similarly, anthropogenic soils in the Amazon and Europe also have elevated nutrients (Lima da Costa and Kern 1999; Blume and Leinweber 2004; Schmidt 2014). Our findings of elevated nutrients in middens along the Chesapeake Bay complement the results from these and other studies, and demonstrate a global, albeit variable (see McMichael et al. 2012), trend of soil enrichment at and around archaeological middens that can subsequently influence the composition and abundance of modern plant

communities. Erlandson (2014) has even suggested that the formation of shell middens and other anthropogenic soils, which increased significantly during the Holocene roughly 10,000 years ago, may serve as a marker for the onset of the Anthropocene.

Plant community structure differed between midden and off-midden sites, especially in cover type. While trees and other woody species dominated off-midden sites, forbs and grasses were more common on middens. Middens also had moderately higher species richness, which is consistent with the observation that the majority of temperate forest diversity occurs within the herbaceous layer (Gilliam 2007). More importantly, almost a third of the species observed occurred only on middens, suggesting that middens increase forest diversity at the landscape scale by creating pockets of herbaceous vegetation in an otherwise forested landscape. These results match those of Vanderplank et al. (2014), who observed higher species richness on one midden complex and a greater number of species with a preference for midden conditions than for the surrounding matrix.

In addition, instead of our patterns diminishing with time, we observed that the most ancient middens were also the most likely to be covered in forbs and grasses and the least likely to have woody vegetation (Figure A1). Although our limited sample size constrains our ability to contrast middens of different ages, these data suggest that the effects of ancient humans on the plant community can persist for over 3,000 years. This long-term persistence of anthropogenic effects is consistent with studies of ancient agricultural practices (Dupouey et al. 2002; Plue et al. 2008). Dupouey et al. (2002), for example, showed that more total species occurred on Roman farmstead sites from AD 50–250 than undisturbed sites (~ 74 species depending on the type of site vs. 72 species in undisturbed sites), but also that 20 % of their total species pool was found only in historically-disturbed sites. Similarly, Plue et al. (2008) found that Gallo-Roman agricultural sites, which have been abandoned for 1,600 years, had higher mean richness than unoccupied sites (37 vs. 23 species) and that 26 % of the total species pool occurred only on the archaeological sites.

Given the close proximity of midden and off-midden sites it is unlikely that many environmental variables differed among sites, including factors like

temperature (Norman 1976; Stalter et al. 1999; Stalter and Kincaid 2004) and wave disturbance (Stalter et al. 1999; Stalter and Kincaid 2004), which have been implicated as drivers of the unique flora on middens. In this study, we focused on soil nutrients, which have been shown to shift competitive dynamics in favor of herbaceous plants compared to woody plants (Fridley and Wright 2012). In addition to elevated cation exchange capacity, pH, and nitrate concentrations, we observed particularly high calcium levels in midden soils. Calcium, due to its relative immobility in the soil and thus general inaccessibility, is thought to limit many important plant functions related to morphology, defense, and physiology, and liming experiments have shown increased plant growth after calcium addition (McLaughlin and Wimmer 1999). Elevated calcium levels in temperate forests have also been linked to increased forb richness of both native and non-native species (Von Holle and Motzkin 2007; Burton et al. 2011). While we cannot directly attribute the observed shifts in plant community structure to any one nutrient, our results suggest that elevated nutrients contributed towards the transition from a primarily woody community to a rich herbaceous one. This result is consistent with the structural carbon-nutrient balance hypothesis (Graves et al. 2006), though not necessarily definitive proof as factors other than carbon nutrient ratio might determine competitive dynamics between woody and herbaceous species (Grime 2001).

Our results, in contrast, were not consistent with the fluctuating resource hypothesis (Davis et al. 2000) as we observed high native cover on middens and no increase in non-native species abundance. This hypothesis posits that communities are more susceptible to invasion when there is an excess of available resources. This can occur if resource use by the resident community decreases (due to disturbance, for example) or if nutrient enrichment exceeds what the resident community can utilize. One of the other published studies to rigorously pair sites with adjacent non-midden sites found a greater abundance of non-native species on middens, particularly non-native annual species (Karalius and Alpert 2010). The difference between our results and those of Karalius and Alpert (2010) may be due to the species assemblage in eastern Mid-Atlantic forested communities versus California grasslands. Whereas annual grasses are common in

California grassland ecosystems, the salt marsh and temperate forest associated with riparian communities along the Chesapeake Bay are dominated by perennial flora, and fewer than 5 % of all plant species identified in this study were annuals. Given that short-lived introduced species are often favored by local disturbance (Grime 2001), the lack of a native/non-native pattern in our study may reflect the general lack of short-lived introduced species that could take advantage of these resource hot spots.

In conclusion, many studies have emphasized the importance of considering past land-use history as a driver of current species diversity and distributions. The majority of these studies, however, focus on relatively recent human practices, including agriculture by European settlers (Bellemare et al. 2002; Mosher et al. 2009; Parker et al. 2010) with fewer studies focusing on more ancient human societies (Dupouey et al. 2002; Plue et al. 2008). Here, we show that the legacy of ancient, pre-European societies is still evident in the structure and diversity of forest communities in the mid-Atlantic. Accounting for historical land-use also offers a remarkable opportunity to test ecological hypotheses over very long time frames. Compared to other ecological experiments, Native American shell middens represent incredibly ancient, replicated—yet underutilized—tests of nutrient enrichment on plant community structure.

More generally our results highlight the importance of considering ancient human practices when trying to explain current patterns of species diversity and abundance. Midden boundaries are not immediately obvious and could be missed by casual observers, leading to erroneous hypotheses about why certain species occur in specific locations. This paper thus contributes to a growing literature showing that human effects exist in areas commonly viewed as relatively natural or wild, and that these effects can persist for over 3,000 years.

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