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High abundance of introduced plants on ancient Native American middens

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Abstract Past land uses by humans can have long-term effects on natural communities. To test the hypothesis that past land use can alter patterns of biological invasion for extended times, we predicted that middens abandoned by Native Americans over a century ago would have high abundances of introduced plants. We measured cover of vascular species and soil characteristics on and off the eight remaining middens in grasslands along 20 km of the northern coast of California. Relative cover of introduced plants was about 20% higher on than off middens, and cover of introduced annuals was about 110% higher. Concentration of inorganic N in the upper soil was twice as high on as off middens and explained about 40% of the variation in cover of introduced annuals. Abundance of shells on middens was correlated with inorganic N, suggesting that present invasion was linked to intensity of past land use. Results confirm that ancient land use by Native Americans is associated with present-day invasion by introduced plants and suggest that persistent elevation of soil N is partly responsible. Land use that elevates nutrient levels may promote invasion far into the future.

Keywords Annual grass · Coastal prairie · Introduced plant · Native American midden · Nitrogen · Northern California

Introduction

Past land use by humans can have long-lasting effects on the natural communities that develop after the land is abandoned. For example, past liming of a Swiss grassland still affects the soil microbial community 70 years later (Spiegelberger et al. 2006), forests on former agricultural fields in New England and Europe are more homogeneous than older forests (Vellend et al. 2007) and differ in species composition (Flinn and Marks 2007), and plant species richness in oak forests in France is higher nearer ancient Roman settlements (Dambrine et al. 2007).

Certain land uses by humans might specifically have long-lasting effects on biological invasion by plants (DeGasperis and Motzkin 2007), defined as plants spreading into a new habitat and having negative effects on existing species or processes. Human use generally increases disturbance and sometimes increases soil nutrient availability, both of which are associated with the establishment and spread of introduced plants (Alpert et al. 2000; Renne et al. 2006; Quinn and Holt 2008), defined as those having been brought into a new habitat by humans.

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There is much evidence that recently disturbed or enriched lands are prone to invasion (Parks et al. 2005; Kulmatiski et al. 2006; Seabloom et al. 2006). Harder to test and less well understood is how long this effect can persist after use stops.

Native American middens along the northern coast of California afford an unusual opportunity to test the hypothesis that human land uses that create disturbance and increase soil nutrients can have long-term effects on invasion by introduced plants, long-term in the sense that effects can be observed many years after a land use ceases. From at least 2000 years ago until the late 1800's, the area was used year-round by Native Americans, most recently by the Pomo and Miwok (Alvarez and Fredrickson 1989; Kennedy 2004). Among the types of archeological sites left from their residency are middens, places on sand dunes and coastal terraces where foods such as mussels and seals that had been harvested from the ocean were cooked and the refuse discarded, a localized land use that seems very likely to have both bared the soil and enriched it with nutrients. Although abandoned for over a century, these middens can still be recognized by accumulations of charcoal and fragments of shells and bones in the soil (Kennedy 2004).

Shell middens created by humans are widespread on the world's coasts and provide an important source of information about past cultures, as for example in Africa (e.g., Tonner 2005), the Middle East (Diedrich 2006), South America (Stattegger et al. 2006), Australia (Rosendahl et al. 2007), and Europe (Van der Schriek et al. 2007). Many coastal shell middens in California consist largely of the remains of mollusks harvested from rocky, intertidal habitats and can yield evidence about human impacts on marine fauna over hundreds to thousands of years (Erlandson et al. 2005; Whitaker 2008; Braje et al. 2009). Inland, non-shell middens can still show altered soil chemistry 800 years after abandonment (King 2008), and reports on the floras of ancient coastal shell middens, defined as those abandoned at least a century ago, in eastern North America show that they can support distinctive present plant communities (Stalter and Kincaid 2004; Kelly 2006). However, no study appears to have asked whether ancient middens are present sites of invasion.

We predicted that the relative cover of introduced plants (i.e., cover of introduced plants as a proportion of cover of all plants) would be higher on than off middens within the same type of vegetation. We further asked if this might be explained by persistent elevation of soil nitrogen availability, and if more intensively used middens, as indicated by abundance of shell fragments, were more highly invaded than less used ones.

Methods

Research was conducted during June and July 2007 in Sonoma Coast State Park and the University of California Bodega Marine Reserve along a 20-km length of the coast of California from the mouth of the Russian River south to Bodega Head, which is about 100 km north of San Francisco. Along most of this coast, small sandy coves and rocky points are backed by bare to brushy cliffs that are 5–50 m high and topped with grassy terraces and brushy gullies extending 0.1–1 km inland to hills. The grassland and shrubland communities have been respectively characterized as coastal prairie and coastal scrub (Heady et al. 1995), both of which are common and widespread along the central coast of California. Except on Bodega Head, soils under the grassland communities are predominantly Rohnerville loams, ranging from sandy clay loams to sandy clays, with moderate permeability and fertility and pH of 5.5–5.7 (Miller 1990); on Bodega Head, grassland soils are well-drained loamy sands in the Baywood Series or Sheridan coarse sandy loams, with high permeability, moderate fertility, and pH of 5.7–6.0.

The area experiences a Mediterranean-type climate, with a cool, rainy winter and a summer drought. As measured on the reserve by the Bodega Marine Laboratory (archived data available at www.bml.ucdavis.edu), mean annual temperature is 11.7°C and mean annual precipitation is 785 mm, entirely as rain. Most of the rainfall (84%) occurs from November through March.

Based on previous studies and their own surveys, Alvarez and Fredrickson (1989) and Kennedy (2004) together identified 22 remaining middens between the Russian River and Bodega Head. We resurveyed the sites of these middens and used all eight that were in grassland and had not been lost to erosion or development. We determined the boundaries of the midden at each site from maps in Alvarez and Fredrickson (1989) and as indicated by blackened soil and shell fragments. We found no conflicts between the maps and our observations, although boundaries were only approximately noted on the maps. Areas of middens ranged from 490 to 3300 m^2 as estimated from ellipses determined by the largest and smallest diameters of each midden. Apart from soil characteristics and shell fragments, middens were not obviously different from surrounding areas; they were not noticeably raised or depressed, and were nearly completely covered by grasses and forbs with a few scattered shrubs, as were the areas around them.

We measured the cover of each vascular plant species by visual estimates in five plots on and six plots off the midden at each site, using 50 × 50 cm plots and cover classes of 0–1, 1–5, 5–10%, and then intervals of 10%. Kolb et al. (2002) found this method to be as accurate as measuring occurrence at points in similar plots in coastal grassland on Bodega Head. To distribute plots evenly on a midden, we located one plot in the center of the midden and four plots halfway from the center to the edge going respectively magnetic north, east, west, and south. Plots off the midden in the adjacent grassland were located 10 m outside the boundary of the midden along radii spaced at 60° intervals starting from north. We identified species and classed them as introduced or native and as annual or perennial following Hickman (1993).

To characterize soils, we collected a core 10 cm deep and 1.7 cm in diameter from the center of each plot on July 16–17 and mixed cores to obtain one sample from on and off each midden. Approximately 20 g of each sample was extracted in 40 ml of 2 M KCl for 24 h, filtered through ashless paper, and analyzed colorimetrically for NO_3 and NH_4 in an autoanalyzer (QuickChem FIA 8500, Lachat Instruments, Loveland, CO, USA). Another 70–130 g of each sample was weighed, dried to constant mass at 60°C, and reweighed to determine water content. As a very limited indication of the total contents of C and N of soils, an additional core was collected on and off of the midden at each of two sites. These cores were ground with a mortar and pestle and dried, and 30 mg of each core was combusted in a Flash EA 1112 series Elemental Analysis system (Thermo Scientific, Waltham, MA, USA).

As an indication of intensity of use, concentrations of shell fragments in the soil on each midden were visually classed as none, low, medium, or high. Although abundance of shell fragments might be determined by factors other than intensity of use, such as erosion or how recently a site was abandoned, we were unable to use a more definitive but destructive method such as excavation because we did not have permission to do so.

For analysis, cover classes were converted to their respective midpoints. Mean cover was then calculated for each species in the five plots on each midden and in the six plots off each midden, and summed by eight categories of species: introduced or native crossed with annual or perennial crossed with graminoid or forb. We encountered two species of shrub, both native, in plots. Shrubs had an overall mean cover of just 0.3%, and we included them in calculations of total cover and cover of natives but did not analyze them as a separate category.

To test effects of location (on or off midden) on the relative cover of introduced species (introduced cover/total cover), we used an ANOVA with site as a blocking effect and location as a fixed effect, an appropriate design for paired observations (Sokal and Rohlf 1995). We used the same model to test effects of location on soil water content and concentrations of NO_3, NH_4, and total inorganic N. To test for effects of location on the eight different categories of species described above, we used an ANOVA with site as blocking effect and location, origin (introduced or native), longevity (annual or perennial), and form (graminoid or forb) as fixed effects. Cover and relative cover were transformed to the arcsine of the square root before analysis; untransformed data are presented in figures. Paired *t*-tests were used to compare cover of selected categories and individual species on and off middens. Relationships between N availability and cover and between shell concentration and cover or N were respectively tested with regression and Spearman rank correlations. Preliminary analyses showed no relationship between the area of a midden and either species composition or soil characteristics, so area was not included as a factor in any tests. Tests were run in SYSTAT 11.0.

Results

As predicted, the relative cover of introduced species was higher on than off middens (Fig. 1); means across sites differed only slightly, but the difference

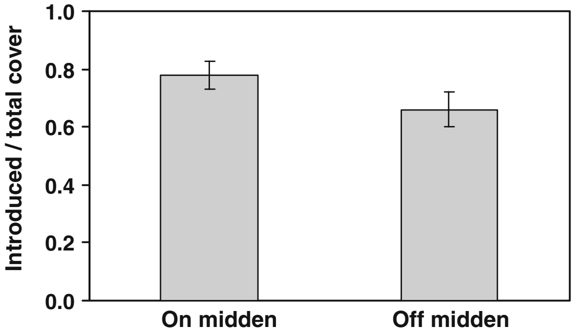

Fig. 1 Relative cover (introduced/total; mean ± SE) of introduced plants on and off middens. ANOVA: block—$F_{7,7} = 13.8$, $P = 0.001$; location (on or off midden)—$F_{1,7} = 16.05$, $P = 0.005$

was highly significant, and the relative cover of introduced species was higher on than off the midden at every site. Higher relative cover of introduced species on middens was due both to higher cover of introduced species [mean difference on minus off middens (SE): 19.5 (6.2) percentage points; P (paired t-test) = 0.017] and to lower cover of native species [−14.4 (3.4); $P = 0.004$].

Effect of location on middens also differed between annuals and perennials, though not between graminoids and forbs (Fig. 2; Table 1: effects of location × longevity and location × form). The cover of annuals, which was almost entirely made up of introduced species, was higher on than off middens [mean difference (SE): 19.3 (6.3) percentage points; P (paired t-test) = 0.017], while the cover of perennials was lower [−14.2 (6.5); $P = 0.005$]. Cover of introduced annuals was about 110% higher on than off middens.

The tendency for annuals to be more abundant on than off middens was consistent among common species (Fig. 3): nine of the ten species of annuals with the highest overall mean covers in plots had a higher cover on than off middens, though individual differences were not significant. All of these annuals were introduced (Fig. 3: legend). Tendency for perennials to be less abundant on than off middens was not consistent: only six of the ten species of perennials with the highest overall covers had a lower mean cover on than off middens. A total of 81 species were found in plots: 53 forbs, 26 grasses, and 2 shrubs. There were fewer introduced (33) than native

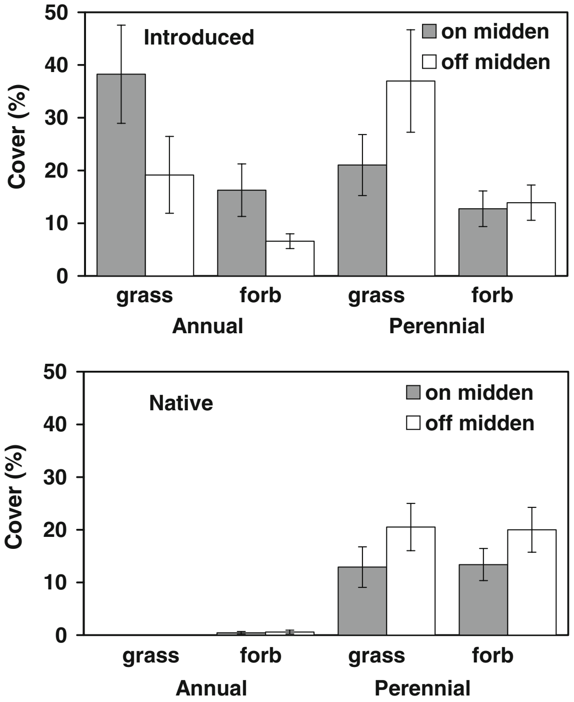

Fig. 2 Cover (mean ± SE) of introduced and native plants on and off middens, by categories of longevity and growth form. Cover of native annual graminoids was zero. See Table 1 for ANOVA

Table 1 ANOVA of effects of block, location (on or off midden), origin (introduced or native), longevity (annual or perennial), and growth form (forb or graminoid) on cover

Effect	*df*	MS	*F*	*P*
Block	7	0.0108	0.24	0.97
Location (l)	1	0.0038	0.09	0.77
Origin (o)	1	*0.6868*	*15.60*	*0.0002*
Longevity (g)	1	*0.4541*	*10.32*	*0.0018*
Form (f)	1	0.1695	3.85	0.053
l × o	1	0.0042	0.10	0.76
l × g	1	*0.2473*	*5.62*	*0.020*
l × f	1	0.0110	0.25	0.62
o × g	1	*0.4211*	*9.57*	*0.0026*
o × f	1	0.1542	3.50	0.064
g × f	1	0.0058	0.13	0.72
Residual	91	0.0440		

Effects with $P < 0.05$ are in italics. Three- and four-way interactions were not significant (each $F_{1,91} < 0.05$, $P > 0.3$) and are not shown

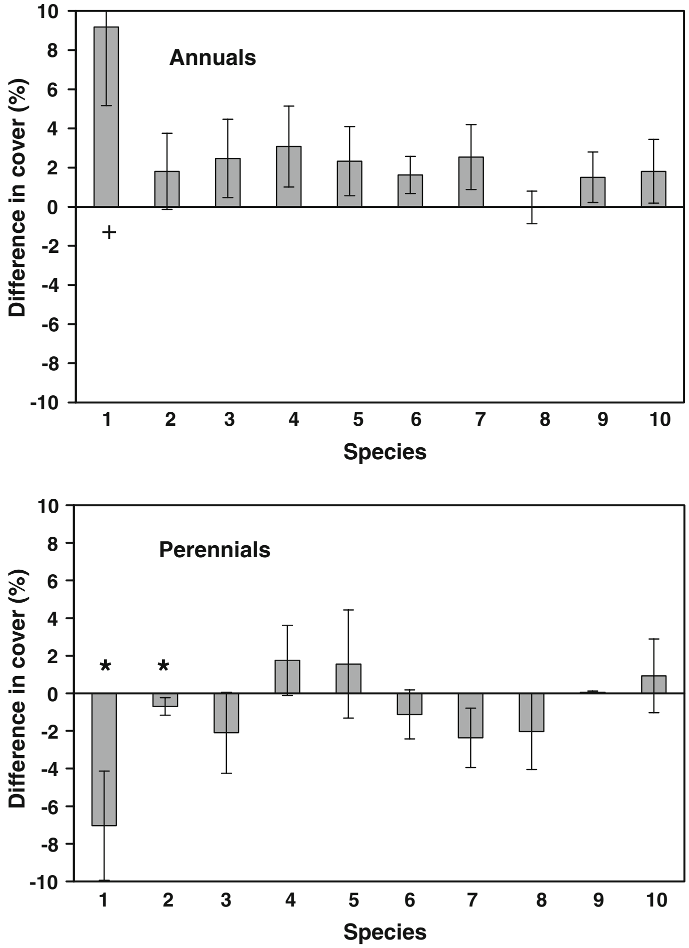

Fig. 3 Difference in cover (mean ± SE) on and off middens of the 10 annual and 10 perennial species with highest overall cover. Annual species (I, introduced; N, native; F, forb; G, graminoid): 1 *Bromus diandrus* (IG), 2 *Lolium multiflorum* (IG), 3 *Briza maxima* (IG), 4 *Vulpia bromoides* (IG), 5 *Geranium dissectum* (IF), 6 *Bromus hordeaceus* (IG), 7 *Medicago polymorpha* (IF), 8 *Cynosurus echinatus* (IG), 9 *Aira caryophyllea* (IG), 10 *Vicia sativa* (IF). Perennial species: 1 *Holcus lanatus* (IG), 2 *Rubus ursinus* (NF), 3 *Plantago lanceolata* (IF), 4 *Carex* sp. (NG), 5 *Rumex acetosella* (IF), 6 *Hypochaeris radicata* (IF), 7 *Danthonia californica* (NG), 8 *Marah fabaceus* (NF), 9 *Leymus pacificus* (NG), 10 *Achillea millefolium* (NF). Symbols show *P* (paired *t*-test): * <0.05; +0.05–0.1; (no symbol) >0.1

species (48), and roughly similar numbers of annuals (39) and perennials (42). Over 80% of introduced species (27) were annual, and over 80% of natives (37) were perennial. Middens contained 0.2–0.3% mean cover of each of three introduced and four native species not found in plots off middens; all of these species occur off middens in coastal prairie in the study area (Kolb et al. 2002; species list for Bodega Head available at www.bml.ucdavis.edu). Plots off middens contained 0.2–1.0% mean cover of each of three introduced and seven native species not found in plots on middens, and contained a mean cover of 2.1% of one additional native species not found off middens. The remaining 63 species were found in plots both on and off middens.

The concentration of total inorganic N in the upper soil was about twice as high on as off middens, due mainly to a threefold higher concentration of NO_3 on middens (Table 2). Soil water content was half as high on as off middens (Table 2). At each of the two sites where total C and N were measured, both were higher on (46–48 mg C/g dry soil; 3.9–4.0 mg N/g dry soil) than off (35–36 mg C/g; 2.8–2.9 mg N/g) middens.

Concentration of total inorganic N explained about 39% of the variation in relative cover of introduced

Table 2 Mean (SE) concentrations of plant-available nitrogen (μg N/g dry mass soil), and water content (g H_2O/g dry mass soil) on and off middens, and results from ANOVAs

	On midden	Off midden	Block		Location	
			$F_{7,7}$	*P*	$F_{1,7}$	*P*
Inorganic N (μg N/g)	17.3 (3.2)	7.8 (1.0)	1.05	0.5	8.16	0.02
NO_3 (μg N/g)	12.4 (3.3)	3.8 (0.9)	1.11	0.4	7.59	0.03
NH_4 (μg N/g)	4.9 (0.5)	4.1 (0.3)	3.87	0.05	4.65	0.05
Water (mg/g)	9 (2.7)	21 (4.0)	1.52	0.3	8.55	0.04

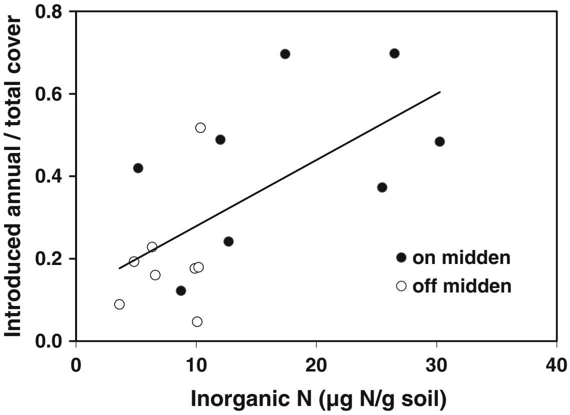

Fig. 4 Relative cover of introduced annuals versus concentration of inorganic nitrogen in soils on and off individual middens. Line shows linear regression of N on all soils: $R^2 = 0.39$, $P = 0.009$

annuals on and off individual middens, assuming a linear relationship (Fig. 4); a logarithmic regression gave only a slightly better fit ($R^2 = 0.42$). On middens, concentration of inorganic N was highly correlated with the abundance of shell fragments in the soil; cover of introduced annuals was marginally correlated with shells (Fig. 5).

Discussion

Results confirmed the prediction that the abundance of introduced plants would be higher on than off middens, supporting the hypothesis that past land use can have long-lasting effects on biological invasion, in this case a positive effect observable after more than a century. The effect was specifically due to invasion by introduced, annual plants; introduced perennials did not have higher cover on than off middens. Although we cannot rule out the possibility that the differences in plant species composition on and off middens were due to human activities since middens were abandoned, these would have had to be activities that were specifically carried out on middens and not immediately adjacent to middens, and we know of no such activities.

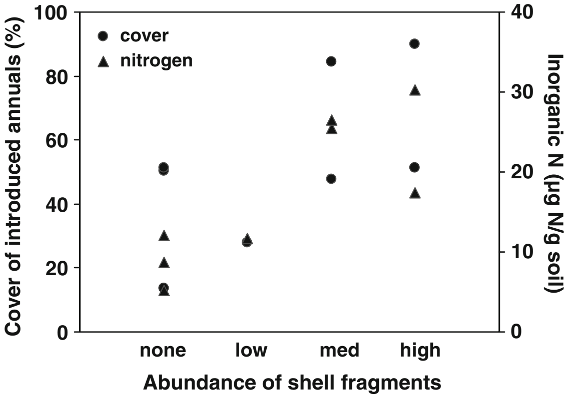

Fig. 5 Relationship between abundance of shell fragments, soil nitrogen (μg inorganic N/g dry mass soil) and cover of introduced annuals on individual middens. Spearman's rank correlation: shells and N—$r_6 = 0.865$, $P < 0.01$; shells and cover—$r_6 = 0.642$, $P = 0.05$–0.1

One likely mechanism for the effects of these ancient middens on present abundance of introduced annuals is persistent elevation of nitrogen availability. Concentrations of inorganic N were higher on than off middens. That this was caused by past human use was supported by the correlation between inorganic N and the apparent intensity of use of middens, as indicated by abundance of fragments of shells of processed food. Concentration of inorganic N explained about 40% of the abundance of introduced annuals on and off middens, and abundance of introduced annuals in Californian grasslands is known to be promoted by high N availability (Kolb et al. 2002; Seabloom et al. 2003; Gea-Izquierdo et al. 2007). Although we measured species composition on middens in only one year, the similar association between high N availability and abundance of introduced annuals in our study and in other studies suggests that our results are not likely to be due to the particular year in which we measured. If elevated N is in fact the cause of high abundance of introduced plants in this system, then other types of middens or middens in other regions might also be expected to show high levels of invasion by introduced plants, to the extent that these middens are enriched in nutrients that limit the spread of introduced species.

An alternative mechanism for high abundance of introduced species on the middens we measured is disturbance, particularly if the introduced annuals were already present when the middens were abandoned. Although none of the annuals appear to have been intentionally introduced, they were almost all European, and some unintentional introductions of European annuals to California are known to have occurred as early as the 1700's (Mensing and Byrne 1999). Introduced annual and native perennial grasses in coastal prairie and similar grasslands in California can show stage-structured competition: when all plants are seedlings, the annuals outcompete the perennials; when the perennials are adults, they outcompete the annuals (Kolb et al. 2002; Corbin and D'Antonio 2004). This could create persistent, alternative states, with introduced species unable to invade well-established stands of natives, and vice versa (Cox and Allen 2008). Unless the bare areas likely to have been left on abandoned middens were colonized by natives well before introduced annuals could disperse in, populations of annuals could establish and then resist invasion by native perennials. The observed correlation between N and abundance of introduced annuals on middens might not be causal, but rather a byproduct of the effects of land use on both disturbance and N; that is, human uses of middens might have promoted abundance of introduced species by creating bare areas, and also elevated N, but without that being the cause of high abundance of the introduced species.

These different possible mechanisms have different implications for attempts to mitigate long-lasting effects of land use on invasion. Other past land uses in other systems have also been shown to affect patterns of nutrient availability for many decades (Fraterrigo et al. 2005; Dambrine et al. 2007; Flinn and Marks 2007). If these patterns are promoting invasion, then mitigation may require active restoration of pre-use nutrient levels. In contrast, if past disturbance coupled with stage-structured competition is promoting invasion, then mitigation may require either removal of introduced plants and seed banks followed by seeding with natives, or else planting of adult natives (Corbin and D'Antonio 2004; Moyes et al. 2005).

In the case of middens in coastal prairie, we believe that elevated soil N is at least partly responsible for persistent effects on invasion. Elevated nutrient levels can override stage-structured competition in this system, enabling introduced, annual grasses to outcompete natives even when natives are present as adults (Kolb et al. 2002; Alpert 2006). It would be interesting in further work to see how present effect on vegetation depends on time since individual middens were abandoned. However, it seems clear from the results here that, in systems where high nutrients favor introduced over native plant species, human land uses that raise nutrient levels may promote invasion far into the future.

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