Reliability of macrofossils in woodrat (*Neotoma*) middens for detecting low-density tree populations

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Abstract.—Macrofossils from woodrat (*Neotoma*) middens serve as an important proxy for reconstructing past vegetation in arid and semiarid regions of North America. The presence/absence of plant macrofossils in middens can provide valuable information on temporal and spatial patterns of plant migration and range boundaries. The primary aim of this study was to determine how local plant abundance, distance of plant populations from midden sites, and species population density on the landscape affect the probability of occurrence of macrofossils in middens. The study was designed with the primary intent of determining the reliability of middens in detecting scattered populations of *Pinus ponderosa*. We analyzed macrofossil assemblages from 42 modern woodrat middens from West Carrizo Canyon in southeastern Colorado, near the current eastern range margin of *Pinus ponderosa*. We compared midden contents with composition of the surrounding vegetation, measuring distance from the midden to the nearest individual of selected plant species, and the percent cover of each species within 30 m of the midden. We used this information to model the probability of species presence in a midden across a range of population densities on the landscape. Macrofossils of *Juniperus* spp., *Quercus gambelii*, and *Opuntia* spp. were consistently found in middens regardless of their local abundance in vegetation, although populations occurred within 30 m of all middens. *Pinus edulis* and *P. ponderosa* occurred in nearly all middens within 20–30 m of individual trees. *P. ponderosa* was rare in middens >20–30 m away from individual trees. Results of a simple simulation model suggest that middens become absolutely reliable indicators of *P. ponderosa* presence on the landscape only when average tree density exceeds 50 stems ha^{-1}. Woodrats reliably collected macrofossils of *Pinus edulis, P. ponderosa, Juniperus* spp., *Quercus gambelii*, and *Opuntia* spp. when populations of these taxa occur within 20–30 m of a midden site. Woodrats did not collect *P. ponderosa* when the nearest individuals were more than 30 m away. Low-density populations of these and other species may be difficult to detect in fossil woodrat-midden series owing to reduced probability that individuals grow within foraging distance of the middens. Data from this and similar studies can be used to construct and parameterize a forward model of macrofossil representation in woodrat middens.

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Introduction

Paleoecological studies are inevitably concerned with documenting past distributions and abundances of species and higher-level taxa. Undetected populations represent a major source of uncertainty, potentially confounding inferences concerning invasion, contraction, speciation, extinction, refugia, community composition, and ecosystem structure. The problem has common features in a wide variety of depositional settings: density and spatial dispersion of populations, population proximity to depositional sites, mechanisms of transport and deposition, and sampling density in time and space all play important roles in representation (Prentice 1985; Dunwiddie 1987; Davis et al. 1991; Greenwood 1991; Jackson 1990, 1994; Sugita 1994; Parshall 1999; Birks 2001; Jackson and Booth 2007; Sugita 2007). Uncertainties arising from these factors and their interactions can be assessed and even quantified, given systematic understanding of the processes and quantitative estimation of potential errors.

Paleoecological studies of terrestrial vegetation since the last glacial maximum are based primarily on pollen and plant-macrofossil studies of lake sediments (Jackson et al. 1997; Williams et al. 2004) and desiccated rodent middens (Betancourt et al. 1990; Betancourt 2004). All pose challenges for detection of scattered, low-density populations. Plant macrofossil assemblages impart high spatial precision, and hence can detect small populations within 10^0–10^2 m of a site (Jackson and Booth 2007). However, low spatial density of samples or depositional sites can lead to high probability that small, scattered, or isolated populations will go undetected. Pollen assemblages

typically integrate vegetation over a broad area (10^3–10^5 m), but cannot routinely distinguish between local and distant populations as pollen sources (Davis et al. 1991; Jackson 1994; Sugita 1994, 2007). These uncertainties have long recognized been, but remain poorly characterized and quantified.

Plant macrofossils from rodent middens constitute the primary source of data on past vegetation composition and species distributions in arid and semiarid regions of the world, and woodrat (*Neotoma* spp.) middens have been extensively used in western North America (Thompson 1988; Betancourt et al. 1990). Individual middens represent ''snapshot'' samples of surrounding vegetation collected by rodents over a period of years to decades. In typical applications, ancient middens are collected from overhangs and crevices within a study area (e.g., a canyon, cliff face, or escarpment), analyzed paleobotanically, radiocarbon-dated, and stacked chronologically to yield an unevenly spaced time series for the site. Midden sequences have been widely applied in biogeographic studies, including patterns of species invasion and extirpation in response to climate change (Cole 1990; Betancourt et al. 1991, 2001; Nowak et al. 1994; Cole et al. 1997; Jackson et al. 2002, 2005; Sharpe 2002; Lyford et al. 2003; Anderson and Feiler 2010).

The middens constructed at any given time undergo steady reduction in number. Most middens will eventually be destroyed by such processes as excavation by subsequent generations of woodrats, decomposition owing to bedrock seepage or rainfall/snowfall exposure, and erosion and spalling of bedrock. Of the fossil middens preserved at a particular site when scientists arrive, some will go undetected or uncollected because of inaccessibility, safety, and other factors. Finally, some collected middens may go undated owing to resource limitations. Thus, the probability that a particular time series will have a midden representing a particular time interval (e.g., a particular century) is low.

For example, the time gap between temporally adjacent middens in 23 Holocene midden sequences averaged 648 years, with average within-series time gaps ranging from 122 to over 2000 years (Table 1). In one of the most intensive midden-sampling efforts to date, Jackson et al. (2005) collected and dated 36 Holocene middens from Dutch John Mountain in Utah. The average time interval between middens was 265 years, but the series has five gaps exceeding 500 years, including a 2200-year gap in the early Holocene (Table 1).

In order to assess the validity of inferences based on presence/absence data in fossil middens, a better understanding of the processes underlying macrofossil representation in middens is needed. Previous studies of modern middens indicate that woodrats are selective in their collection of plant species on the surrounding landscape (Cole and Webb 1985; Dial and Czaplewski 1990; Spaulding et al. 1990; Frase and Sera 1993; Nowak et al. 2000; Lyford et al. 2004; Fisher et al. 2009). Some species, particularly *Juniperus* spp. and other conifers (*Pinus* spp., *Pseudotsuga*, *Ephedra*), are consistently represented in middens when they occur in surrounding vegetation (Lyford et al. 2004). However, the effects of density and dispersion, particularly distance of individuals from midden sites, remains poorly assessed for these and other species (Lyford et al. 2004). Determination of the distances within which woodrats will collect particular plant species in various settings will allow estimation of uncertainties in paleoecological inferences.

In this study we investigate the effects of population abundance and dispersion on macrofossil representation in modern woodrat middens in West Carrizo Canyon in southeastern Colorado. Our study focuses on *Pinus ponderosa*, although it also provides information on representation of *P. edulis* and other woody and non-woody species. The canyon is representative of fossil-midden study sites; midden sequences spanning most of the Holocene have been obtained (Feiler 1994; Anderson and Feiler 2010; Lesser et al. unpublished). Active woodrat middens are abundant throughout the canyon, and *P. ponderosa* and *P. edulis* occur in scattered populations in several reaches of the canyon. This provided a natural experimental setting by which we could select middens at varying distance from the nearest individuals of these species, and with varying

TABLE 1. Time span between Holocene middens taken from 23 midden series across western North America. Mean and median time spans are shown as well as the maximum and minimum time span between temporally adjacent middens.

Midden series	Time between middens (yrs)*				No. of middens	Oldest Holocene midden (cal. yr B.P.)	Source
	Mean	Median	Min.	Max.			
Diamond Craters, Ore.	122	75	10	400	24	4075	Mehringer & Wigand 1990
East Pryor Mountains, Mont.	185	138	0	710	33	6420	Lyford et al. 2003
Lower Canyon Creek, Wyo.	203	213	30	370	7	1820	Lyford et al. 2003
Wind River Canyon, Wyo.	213	147	0	883	19	3876	Jackson et al. 2002
Twin Creek, Wyo.	263	130	60	980	7	1875	Lyford et al. 2003
Dutch John Mountain, Utah	265	175	5	2240	36	9485	Jackson et al. 2005
Rough Canyon, N. Mex.	337	205	15	980	23	7610	Betancourt et al. 2001
Owl Canyon, Colo.	356	85	0	1310	15	5090	Betancourt et al. 1991
Buffalo Creek Lookout, Wyo.	389	263	5	875	9	3280	Lyford et al. 2003
Big Pryor Mountains, Mont.	392	165	0	2750	24	9545	Lyford et al. 2003
Brokenback Canyon, Wyo.	463	290	120	1180	8	3355	Lyford et al. 2003
Titus Canyon, Calif.	604	510	12	1838	16	9751	Smith et al. 2009
Mahogany Butte, Wyo.	647	445	75	1915	14	8410	Lyford et al. 2003
West Carrizo Canyon, Colo.	647	714	60	1255	11	6839	Anderson and Feiler 2010
Medicine Lodge Canyon, Wyo.	662	320	25	2695	12	8600	Lyford et al. 2003
Fremont Canyon, Wyo.	674	360	10	2685	14	8930	Lyford et al. 2003
Hartnet Draw, Utah	779	390	255	1835	8	5450	Cole et al. 1997
Pichacho Peak, Calif.	798	295	100	4170	13	9590	Cole 1990
Birdseye Creek, Wyo.	826	608	5	2095	5	3350	Jackson et al. 2002
Tweaver Pass, Wyo.	880	855	710	1100	5	4545	Lyford et al. 2003
Meyer Spring Draw, Wyo.	1027	750	290	2030	6	5425	Lyford et al. 2003
Painted Hills, Nev.	1692	1020	200	4490	6	9640	Nowak et al. 1994
Dinosaur National Monument, Colo.	2468	1910	590	5460	5	9870	Sharpe 2002
Overall†	648	437	112	1924			

* Midden series were truncated to last Holocene midden (10,000 cal. yr BP) for the analysis.

† Overall values calculated as average across all midden series.

population sizes in the immediate vicinity of the middens. Specifically, our study was designed to determine (1) effects of distance from the midden site to the nearest individual of these species on macrofossil representation, and (2) effects of local abundance of these and other species on macrofossil representation. Our data also provide additional information on woodrat foraging and collection preferences in a particular vegetational setting, contributing to assessment of whether woodrat collection foraging for particular species depends on the array of species represented in the vegetation (Lyford et al. 2004). We use our results to model the reliability of an individual midden assemblage in detecting *P. ponderosa* at varying average population densities, and apply our model results to the general problem of detecting low-density populations in the paleoecological record.

Methods

Study Design.—The study site was in West Carrizo Canyon (37°6′20.88″N,103°9′7.56″W),

southeastern Colorado (Fig. 1). Modern middens were collected from the east and west ends of the canyon (Fig. 1), where fossil middens were concentrated. The rimrock of West Carrizo Canyon is formed by Dakota Sandstone (Cretaceous), underlain by Purgatoire Shale (Jurassic) (Fenneman 1931; Scott 1968). Middens are abundant in crevices and fractures in the Dakota Sandstone exposures.

The dominant tree species at the site include *Juniperus monosperma* (Engelm. [Sarg.]), *Juniperus scopulorum* (Sarg.), *Pinus edulis* (Engelm.), and *Pinus ponderosa*. All of these species occur at low densities (<30 trees ha^{-1}), and *Pinus ponderosa* occurs only in small, widely scattered clusters. Other dominant species include *Quercus gambelii* (Nutt.), *Rhus trilobata* (Nutt.) and *Opuntia* spp. (both prickly-pear [*Opuntia polyacantha* (Haw.)] and cholla [*Opuntia imbricata* (Haw. [DC.])] growth forms). *Quercus gambelii* is present in dense thickets throughout the canyon. Three species of woodrats may occur within the study area: *Neotoma mexicana* (Mexican wood rat), *Neotoma albigula*
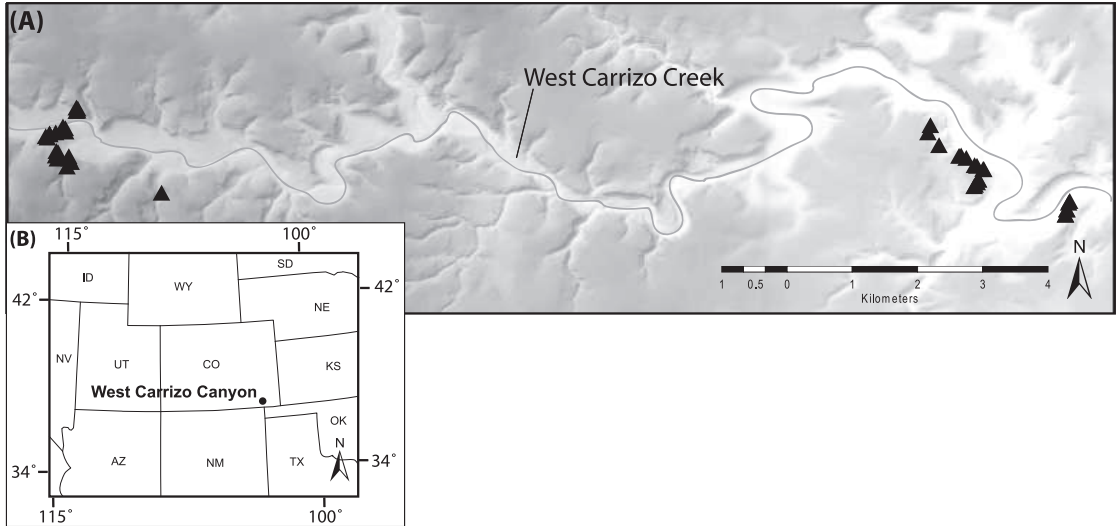
FIGURE 1.   Map of study area. A, Individual midden locations within West Carrizo Canyon. B, Regional location of West Carrizo Canyon.

(white-throated wood rat), and *Neotoma micropus* (gray wood rat) (Finley 1958). Of these, *N. mexicana* is most likely the dominant species in the *Pinus/Juniperus* woodlands of the canyon (Finley 1958; F. Smith personal communication 2010). Furthermore, in eastern Colorado, *N. mexicana* is also commonly associated with vegetation dominated by *Quercus gambelii* and scattered *Pinus ponderosa* (Finley 1958). The other two species (*N. albigula* and *N. micropus*) prefer cactus-grass vegetation, making them less likely to occur in West Carrizo Canyon. However, *N. albigula* will venture into cactus-juniper woodlands on rocky slopes (Finley 1958), and thus we cannot completely rule out its presence in our study area.

The study was designed with the primary intent of assessing effects of distance and abundance of scattered populations of *Pinus ponderosa* on representation in middens. Modern middens were selected across a range of distances to the nearest *Pinus ponderosa* individuals (0 m to >100 m in as evenly spaced intervals as the natural setting would allow). Within this primary objective, we also attempted to collect middens that ranged widely in distance to the other dominant woody species at the site: *P. edulis*, *Quercus gambelii*, and *Juniperus* spp. Distance to the nearest individual of each of these species was recorded for each midden. Data on percent cover were also collected for all succulents and woody species occurring within 30 m of the midden.

Field and Laboratory Methods.—Forty-two middens were collected from West Carrizo Canyon (Fig. 1, Table S1). Only middens that showed evidence of current or very recent use (fresh green plant material, lack of crystalline urine) were selected. The presence of nearby fresh scent posts, undesiccated plant material, and soft fecal pellets also indicated ongoing woodrat activity (Fisher et al. 2009; Lyford et al. 2004). We also chose only middens in locations similar to those in which ancient middens occurred (i.e., crevices, overhangs, and small rock shelters).

We collected plant material, fecal pellets and other debris from the midden while avoiding the actual nest material, which is rarely preserved in ancient middens (Dial and Czaplewski 1990; Frase and Sera 1993; Lyford et al. 2004). Midden material was collected with a spade (head size 18 × 22 cm), with ~8000 cm^3 (two spade scoops) being collected per midden. Using the midden as a center point, the immediate cliff face as one axis, and a line perpendicular to the cliff face as the second axis, we divided the surrounding area into quadrats. Within each quadrat we ran a 30-m line transect on a randomly determined azimuth between 0 and 90 degrees. Line-intercept transects were used to estimate

percent cover for all perennial woody species within 30 m of each midden (Mueller-Dombois and Ellenberg 1974). We also measured the distance to the nearest individual of each primary woody species (Table S1).

Midden material was visually inspected in the laboratory, and plant organs of select species were identified and classified as absent or present (Table S2 lists plant organ types identified for each species). We assessed probability of species occurrence in the midden on the basis of both the distance of the nearest individual of the species to the midden and the percent cover of that species in the surrounding vegetation. *Juniperus* spp. (*Juniperus monosperma* and *Juniperus scopulorum*) were pooled for analysis, because the species did not differ in their occurrence patterns. We also pooled *Opuntia* spp. for the analysis because it is not possible to differentiate species for most macrofossils.

Model Simulations.—We developed a simple stochastic spatial model to estimate the probability of *Pinus ponderosa* occurrence in the midden based on differing densities (trees ha^{-1}) on the landscape. We parameterized the model using our results on foraging distance for *P. ponderosa*. A midden was placed at the center of a virtual landscape 1 ha in size, and partitioned into 1 × 1 m grid cells. We randomly placed individual trees on the virtual landscape at densities ranging from 1 to 70 trees ha^{-1} and calculated the number of individuals that fell within 20 m of a midden (upper quartile distance for presence of *P. ponderosa* in a midden).

The model was further refined to include the probability of presence in the midden even when *Pinus ponderosa* occurred within 20 m of the midden. Each individual tree that fell within 20 m of the midden was assigned a probability of being collected based on our distance data results; thus lowering the overall probability of occurrence in the midden. For all simulations, we ran 100,000 iterations of each tree density and calculated the mean and 95% confidence intervals.

Results

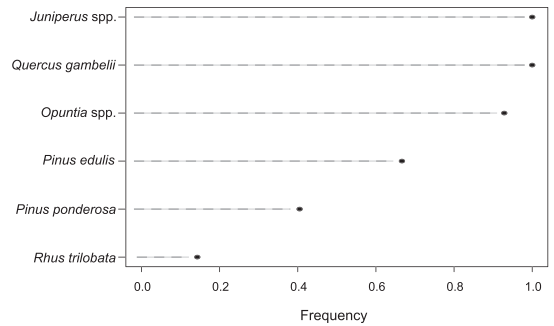The frequency of species occurrence in middens ranged from nearly zero to one

FIGURE 2. Frequency of occurrence of selected plant species in middens, calculated as the number of middens in which that species occurred divided by the total number of middens collected (42).

(Fig. 2). *Juniperus* spp. and *Quercus gambelii* were present in every midden we examined. *Opuntia* macrofossils also occurred in nearly every midden. *Pinus edulis* occurred in over half of the middens, *P. ponderosa* occurred in 0.4 of the middens, and *Rhus trilobata* was extremely rare (Fig. 2).

Effects of Distance.—The probability of *Pinus ponderosa* occurrence in a midden was strongly influenced by distance of the nearest individual from the midden. The median distance of a *P. ponderosa* tree from a midden containing *P. ponderosa* macrofossils was 14.2 m (Fig. 3). Middens lacking *P. ponderosa* were on average further from the nearest *P. ponderosa* tree. Analysis of variance (ANOVA) on presence of *P. ponderosa* against distance of the nearest individual (results not shown) showed that distance of *P. ponderosa* from the midden was a significant factor ($p < 0.001$). ANOVA results showed that the distance of all other species from a midden, including interaction terms between species, were insignificant. However, the relationship between distance to the nearest *P. ponderosa* and presence in a midden was not perfect; six middens lacking *P. ponderosa* macrofossils were within 20 m of a *P. ponderosa* tree, yielding a probability of 0.72 that the species will be represented in a midden given occurrence within 20 m (Figs. 3, 4). Probability of *P. ponderosa* occurrence in a midden drops sharply when the nearest tree is >20 m from the midden and reaches zero at 45 m (Fig. 4).

Foraging distances for *Pinus edulis* are less clear (Figs. 3, 4). Although the median
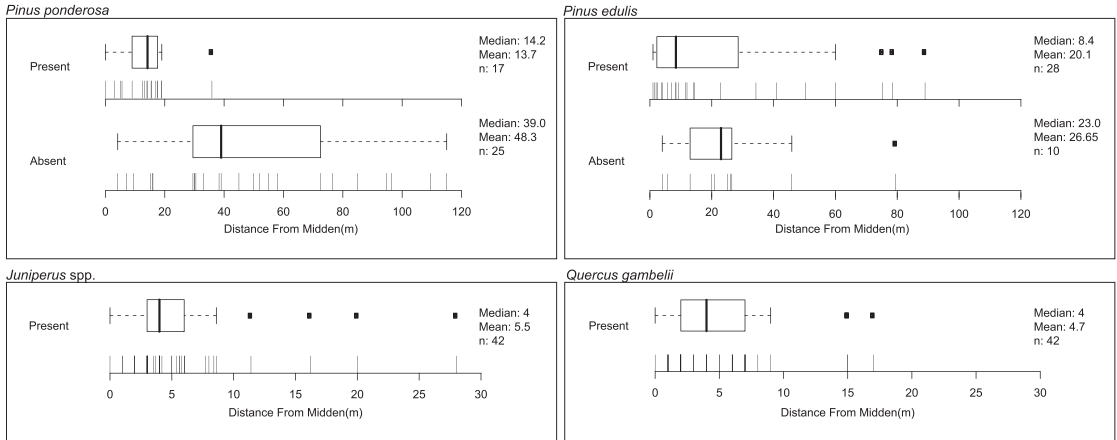
FIGURE 3. Boxplots of presence/absence distribution of macrofossils of individual species in middens plotted against the distance in meters of the nearest representative of that species, in the surrounding vegetation, from the midden. The box represents the first and third quartiles. The whiskers extend to the largest/smallest data point that falls within 1.5 times the box length from the nearest edge. The thick black bar is the median point of the data. Outliers are represented by black squares. All data points are shown as bars along the x-axis. Note scale differences between species.

distance of a midden with *P. edulis* macrofossils from the nearest tree was 8.4 m, *P. edulis* occurred in many middens where the nearest tree was 40–90 m away (Fig. 3). At the same time, *P. edulis* macrofossils were absent from many middens despite occurrence of trees within 20–30 m (Fig. 3). Although our results suggest that probability of occurrence is high (>0.50) given trees >30 m from the midden,
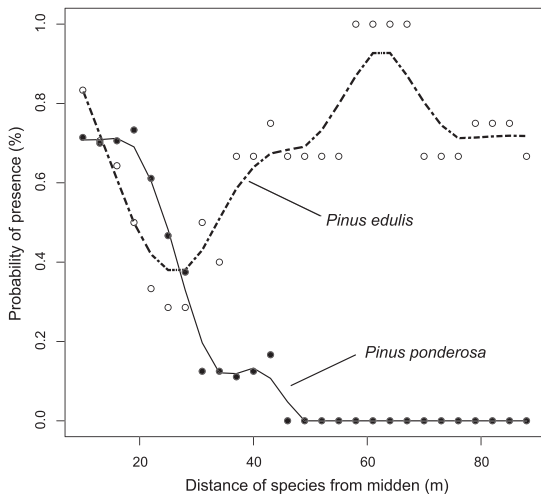

FIGURE 4. Probability of species presence in the midden as a function of distance of that species from the midden. Values are based on a 20-m moving window in 3-m steps. Solid and open circles represent *Pinus ponderosa* and *P. edulis*, respectively. Trend lines are fitted on the basis of a Lowess smoothing function in R. The solid line represents *Pinus ponderosa* and the dashed line *Pinus edulis*.

our sample size for those distances is small ($n = 9$) (we could find few middens situated more than 20–30 m from *P. edulis* individuals). Nonetheless, woodrats will apparently range further from midden sites to collect *P. edulis* than *P. ponderosa*.

Juniperus spp. and *Quercus gambelii* occurred in all 42 middens. However, both taxa were so widespread in the canyon that we were unable to sample middens where individuals were >20–30 m away (Fig. 3). Within these relatively short distances, woodrats collect these taxa with 100% fidelity. This contrasts with both *Pinus edulis* and *Pinus ponderosa*, which had a 0.6–0.8 chance of midden representation within the same distances (Fig. 4). However, *Juniperus* spp. and *Q. gambelii* were generally much more abundant than either of the *Pinus* species within these short distances (Table S1).

Effects of Abundance.—Species abundance within 30 m of midden sites had no major effect on occurrence in the middens, as long as individuals of the species were present within that distance (Fig. 5). ANOVA results (Table 2) confirmed this finding for *P. ponderosa*, showing that local abundance of *P. ponderosa* was significant ($p < 0.001$), but only between zero local abundance (absence) and any amount greater than zero (presence). The sole exception to this pattern for woody species was *Rhus*
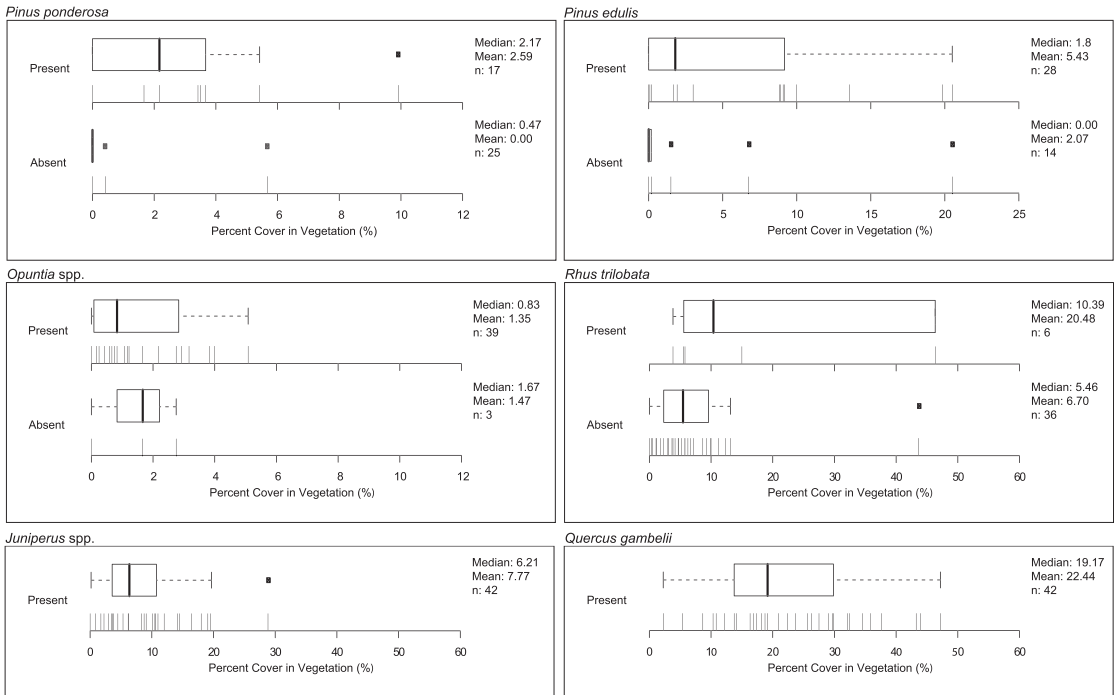
FIGURE 5. Boxplots of presence/absence distribution of individual species in the midden plotted against the percent cover of that species in the surrounding vegetation. See Figure 2 caption for details. Note scale differences between species.

trilobata, which was absent from middens even when local abundance was high (Table 3, Fig. 5). Local abundance of *Q. gambelii* was found to be significantly related to *P. ponderosa* presence in a midden (Table 2); when local abundance of *Q. gambelii* was below 20% it was more likely that *P. ponderosa* would be found in a midden. However, of the 25 middens with >20% *Q. gambelii* in the surrounding area, only ten contained *P. ponderosa*, leaving this result inconclusive. Furthermore, the midden with the lowest abundance of *Q. gambelii* in the surrounding 30 m did not contain *P. ponderosa* (Table S1).

Opuntia was also well represented in middens regardless of local abundance (Fig. 5). It occurred in more than 90% of middens for which *Opuntia* was effectively absent within the surrounding 30 m (Table 3).

Pinus ponderosa and *P. edulis* show similar patterns in relation to local abundance. If no trees occurred within 30 m, the probability of presence in the midden was low. Probability of midden occurrence increased substantially when trees were present within 30 m, but

did not continue to increase substantially as abundance increased (Table 3, Fig. 5).

Model Simulations.—When the only factor considered is distance of the nearest individual from the midden, the probability of *Pinus ponderosa* occurrence in the midden reaches unity at densities of 40 trees ha^{-1} (Fig. 6). When the probability of *P. ponderosa* presence within the 20-m distance radius (prob. 0.72, Fig. 4) is included in conjunction with distance, a threshold level of 50 trees ha^{-1} is required to reach a probability of one for *P. ponderosa* occurrence in the midden (Fig. 6). In both situations, the probability of occurrence decreases at an increasing rate for tree densities below this threshold value. At densities below 10 trees ha^{-1}, *P. ponderosa* has a less than 0.5 chance of being present in the midden (Fig. 6).

Discussion

Representation of Macrofossils.—Unlike macrofossil assemblages in lake sediments, the macrofossils contained in woodrat middens are the result of both physical and behavioral

TABLE 2. Analysis of variance (ANOVA) of *P. ponderosa* presence in a midden against study species local abundance. Only main effects are shown due to all interactions being insignificant.

Source	df	Sum sq	Mean sq	*F*-value	Pr(>*F*)
P. ponderosa abundance	1	1.966	1.966	10.035	0.003**
P. edulis abundance	1	0.130	0.130	0.663	0.421
Juniperus spp. abundance	1	0.100	0.100	0.511	0.488
Q. gambelii abundance	1	0.995	0.995	5.080	0.031*
Rhus trilobata abundance	1	0.005	0.005	0.026	0.872
Opuntia spp. abundance	1	0.067	0.067	0.343	0.562
Residuals	35	6.856	0.196	NA	NA

** sig. at 0.001, * sig. at 0.01.

processes (Lyford et al. 2004). Representation of macrofossils in middens depends in part on the desirability of plant organs of particular species to individual woodrats. The distance a woodrat must travel and the risk it must incur to obtain certain species must be weighed against the potential benefits (Lyford et al. 2004). Although previous studies have addressed representation of plant macrofossils in woodrat middens (Cole and Webb 1985; Dial and Czaplewski 1990; Spaulding et al. 1990; Frase and Sera 1993; Nowak et al. 2000; Lyford et al. 2004; Fisher et al. 2009), relatively few studies have specifically addressed woodrat foraging preferences. Lyford et al. (2004) identified local species density and distance from the midden as important factors affecting representation. However, their study was focused explicitly on juniper-dominated woodlands in Wyoming and adjacent Utah and

TABLE 3. Probability of species presence in a midden based on its percent cover within a 30-m radius.

Species	Percent cover	No. of middens	Probability of presence
Pinus ponderosa	0%	29	0.24
	0.1–5%	7	0.86
	5.1–10%	6	0.67
Pinus edulis	0%	20	0.50
	0.1–5%	8	0.75
	5.1–10%	8	0.88
	10.1–15%	3	1.00
	15.1–20%	1	1.00
	20.1–25%	2	0.50
Rhus trilobata	0%	3	0.00
	0.1–5%	15	0.07
	5.1–10%	14	0.14
	10.1–15%	7	0.14
	>40%	3	0.67
Opuntia sp.	0%	11	0.91
	0.1–5%	30	0.93
	5.1–10%	1	1.00
Juniperus sp.	0–20%	42	1.00
Quercus gambelii	0–50%	42	1.00

Montana, and they noted that different combinations of species may influence foraging preferences. Furthermore, although Lyford et al. (2004) analyzed the effect of local abundance of selected species on presence/absence in a midden, they did not directly address issues of foraging distance in their study. Our study was designed to test for foraging preferences, specifically addressing the distance woodrats will travel from a midden to collect *Pinus ponderosa* and other species.

Our results show that distance of the nearest tree from a midden is important, and that woodrat middens at our study site have a very low probability of containing *Pinus ponderosa* if the nearest individual is more than 20 m away from the midden (Fig. 4). Our results show that woodrats potentially forage much farther for *Pinus edulis* (Figs. 3, 4). This may be due to the higher nutritional value of *P. edulis* seeds (Vander Wall 1997). However, the greater distances that woodrats traveled to collect *P. edulis* could also be due to the absence of other more desirable species in the local vegetation. The pattern of initially decreasing and then increasing probability of *P. edulis* presence in middens as distance from the midden increases (Fig. 4) could also be a result of sampling middens built by different woodrat species (Dial and Czaplewski 1990; Vaughan 1990). Although *Neotoma mexicana* is the most likely midden-builder in the canyon, we cannot rule out the other two species in the region, especially *N. albigula*, which may have different foraging preferences. The paucity of information on foraging behavior and preferences leaves us unable to further clarify these questions.

Our results are consistent with those of Lyford et al. (2004), who found that *Pinus*
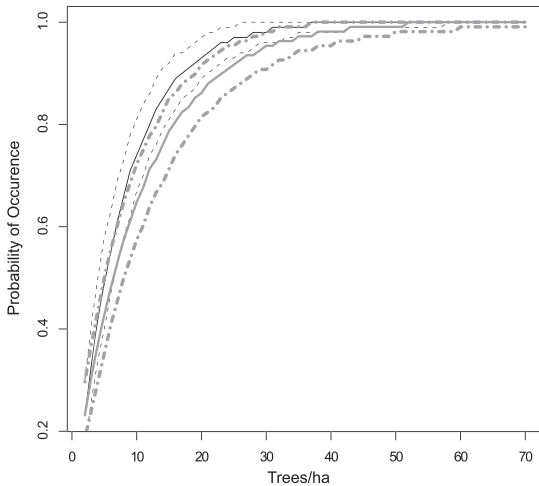
FIGURE 6. Simulated probability of *Pinus ponderosa* occurrence in a midden based on the density of *Pinus ponderosa* in the surrounding area (thin black line); and the density of *Pinus ponderosa* in the surrounding area combined with the probability that a woodrat will collect *Pinus ponderosa* (0.72) when it is within the foraging range (thick gray line). The 95% confidence intervals are shown by dashed lines.

ponderosa and *P. edulis* were well represented in middens where they occurred within 50 m, regardless of their abundance in local vegetation. Furthermore, our results generally confirm that local abundance does not strongly influence species presence/absence in a midden (Lyford et al. 2004). However, the difference in distance that the woodrat is willing to travel to forage for these particular species may be contingent on the suite of species present at the site for the woodrat to choose from. *Quercus gambelii* was absent from all sites of Lyford et al. (2004). Our results show that *Q. gambelii* is consistently collected by woodrats, and this may be at the expense of other species like *P. ponderosa*. We cannot determine whether *P. ponderosa* representation in middens is contingent on presence of *Q. gambelii* or *Juniperus* spp. in the surrounding vegetation. We were unable to find middens lacking *Juniperus* or *Q. gambelii* in our study area, or middens that were >30 m from populations of these species.

Implications of Low-Density Populations.— Our data show that some species (e.g., *Pinus ponderosa*) are poorly represented in middens more than 20–30 m away from the nearest individual. Thus, when population densities

on the landscape are low or locally concentrated, many middens will lack macrofossils of that species. Furthermore, the probability that any particular 50-, 100-, or even 500-year period is represented in a midden time series is low (Table 1). Together, these factors mean that low-density populations, even if persistent for centuries or more, may go undetected in midden records. *P. ponderosa* populations routinely occur on the landscape at low densities, especially at or near the range margins of the species (Kaye et al. 2010). Our model results suggest that there is a high probability that these populations would go undetected in the midden record.

We modeled *P. ponderosa* presence on the landscape as a completely random process. However, in many environments (e.g., West Carrizo Canyon), *P. ponderosa* occurs in clusters controlled by bedrock outcrops, slope and aspect, and drainage patterns. Our model assumption of random distribution of trees likely overestimates the probability of *P. ponderosa* macrofossil occurrence in middens. Conversely, the model may underestimate representation if middens were concentrated in the same areas as the trees. Further studies are required to provide additional empirical basis to the model results we provide here. Refinement of the model to include species contingencies, realistic midden locations, and a broader array of sites would allow more generalizations to be made from our results. However, even with these shortcomings, the simple model we present here demonstrates the potentially poor performance of middens in detecting low-density populations.

Low-density populations may persist on the landscape for a variety of reasons. Unfavorable environmental conditions and/or interspecific competition may restrict populations to isolated microhabitats or simply to low numbers. Populations, particularly near their range margins, may be demographic sinks, where environmental variations allow periodic recruitment but not sustained population growth (Gaston 2003; Jackson et al. 2009). Microsite limitations may limit population growth (Crawley 1990), and propagule availability may interact with microsite availability to limit population growth (Eriksson

and Ehrlén 1992). Allee effects can also restrict populations to low densities for long periods of time (Allee 1931; Stephens et al. 1999).

Colonizing populations also occur, at least initially, at low densities. Population growth and spread may be limited by local disturbance, propagule flux-density from distant sources, unfavorable environments, Allee effects, and extended lag-phase of exponential population growth in species with delayed reproductive maturity (Shigesada and Kawasaki 1997; Gaston 2003; Jackson et al. 2009). For example, demographic data from disjunct range-margin populations of *Pinus ponderosa* in north-central Wyoming indicate that it may take centuries for populations to reach threshold densities for reliable detection by middens (Lesser and Jackson unpublished).

If colonizing populations require multiple centuries to attain densities sufficient to ensure representation in middens, then fossil midden series may underestimate timing of population establishment to some extent, and midden-based maps may underestimate range margins. The extent of these problems is difficult to determine, but empirical observations from modern populations and fossil-midden series suggest that uncertainties are on the order of tens to hundreds, not thousands, of years.

First, although many species exhibit a pattern of decreasing density at their range margins (MacArthur 1972; Brown et al. 1996; Gaston 2003), other species do not (Sagarin et al. 2006; Gaston et al. 2008). Dendroecological studies have shown that woody species, including *Pinus ponderosa* and *P. edulis*, can develop extensive, dominant populations within two to three centuries (Swetnam and Betancourt 1998; Brown and Wu 2005; Brown and Cook 2006; Gray et al. 2006). Repeat photography also reveals that *Pinus edulis*, *P. ponderosa*, and *Juniperus* spp. have invaded new sites and developed dense woodlands within the last 100–125 years in parts of the western United States (Swetnam et al. 1999; Gruell 1980, 1983; Veblen and Lorenz 1991; Betancourt and Jackson unpublished). Second, chronological reversals of presence/

absence of *Pinus edulis, P. ponderosa,* and *Juniperus* spp. are rare in woodrat-midden records (e.g., Lyford et al. 2003; Jackson et al. 2005), indicating that these species reach detectable densities across entire midden sites within the average time interval between adjacent middens in the time series.

The Meaning of Absence in a Midden Assemblage.—Absence of *Pinus ponderosa* or any other species from a midden assemblage may indicate that the species did not occur anywhere near the site at the time of midden construction, or that it occurred near the site but was not collected in the midden because of low population density, woodrat foraging choices, or other factors. Without additional information, absence imparts a deep ambiguity in a data set. The ambiguity of inference from absence is widely recognized in the environmental sciences; Fægri and Iversen (1964) downplayed macrofossil analysis for precisely this reason. It also partly underlies the Signor-Lipps effect, which is widely discussed in pre-Quaternary and extinction paleontology (Signor and Lipps 1982; Holland 1995).

In the face of absence data, paleoecologists have chosen either to rely solely on occurrence data or to assign informal weights or formal probabilities to absence data on the basis of understanding of taphonomy and representation. An example of the first instance is Thompson's (1988) review of woodrat-midden records from western North America, in which only presence data are mapped or plotted. Other examples of using presence-only data in species distribution models include Elith et al. (2006) and Phillips and Elith (2008). This conservative approach, however, may underutilize information and leads to its own ambiguities—for example, voids in a map could indicate absence of sites or absence of occurrences. In the second approach, absences are plotted and inferences, based on external knowledge of the likelihood that a species will be represented in a fossil assemblage given its local occurrence, are drawn. For example, Lyford et al. (2003) drew inferences from absence of *Juniperus osteosperma* in fossil woodrat-midden series based on its 100% occurrence in modern middens within

50 m of individual trees, and others (Jackson et al. 1997; Binney et al. 2009) mapped absence of selected taxa from lake-sediment assemblages based on their high likelihood of occurrence given occurrence of local populations.

Conclusions

Our study demonstrates that distance matters in representation of many species in midden macrofossil assemblages. Local abundance appears to be less critical for most species; occurrence of no more than one nearby individual is sufficient to ensure occurrence in a midden. Absence of a species from a midden assemblage is not a clear indicator of its absence from surrounding vegetation, particularly if populations were at the low densities often associated with initial site colonization.

This study represents an initial step toward quantifying the uncertainty associated with absence of one species, *P. ponderosa*, from a midden. The probability of true absence of a species from the surrounding area given its absence from a midden can be predicted as a function of average population density. Estimation of population growth rates under different scenarios can be used to place confidence intervals on arrival times inferred from middens assemblages. Although it is often difficult to obtain population growth estimates for long-lived tree species, natural invasions and range expansions offer opportunities for direct estimation.

Paleoecological and biogeographic inferences from fossil assemblages are central challenges for paleobiology, and taphonomic studies and modeling are important for estimating reliability and uncertainty in these applications. Rodent middens constitute a major source of paleoecological and biogeographic inference in arid and semiarid regions, informing important questions in climate-change ecology, invasion biology, and community dynamics. Modern rodent middens offer ample opportunities for understanding the taphonomic processes underlying the fossil midden record, and for quantifying the uncertainties in ecological and biogeographic inferences. Our study constitutes a step toward developing and populating a forward model of macrofossil representation in middens.

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Supplementary Information

Additional supporting information can be found at Dryad (doi:10.5061/dryad.187k0).

TABLE S1. Location, presence/absence of species, abundance (%) of species in 30 m surrounding midden and distance of nearest individual of a species to the midden for 42 collected middens.

TABLE S2. Plant organs identified in middens for each target species.