Prehistoric Decline in Freshwater Mussels Coincident with the Advent of Maize Agriculture

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Abstract: *During late prehistory, high population densities and intensive agricultural practices of Native American societies had profound effects on the pre-Columbian landscape. The degree to which Native American land use affected aquatic ecosystems is unknown. Freshwater mussels are particularly sensitive harbingers of modern-day ecosystem deterioration. We used data from prehistoric Native American shell middens to examine prehistoric trends in abundance of freshwater mussels of the genus* Epioblasma *in North America during the last 5000 years. The relative abundance of* Epioblasma *declined steadily during this period, a result that could be explained either by an increase in human impacts to streams or by long-term climatic changes unrelated to human activities. The rate of decline of* Epioblasma *increased significantly, however, after the advent of large-scale maize agriculture in the southeastern United States about 1000 years before the present. Our results suggest that human land-use activities in prehistory caused changes in freshwater mussel communities that were lower in magnitude but similar in direction to changes caused by recent activities.*

Key Words: *Epioblasma*, freshwater diversity, prehistoric human impacts

Declinación Prehistórica en Mejillones de Agua Dulce Coincidente con la Llegada de la Agricultura de Maíz

Resumen: *Durante la prehistoria tardía, las altas densidades poblacionales y las prácticas agrícolas intensivas de las sociedades nativas de América tuvieron efectos profundos sobre el paisaje precolombino. Se desconoce el grado en que el uso del suelo por americanos nativos afectó a ecosistemas acuáticos. Las almejas de agua dulce son indicadores particularmente sensibles del deterioro actual de ecosistemas. Utilizamos datos de restos de conchas prehistóricas para examinar patrones de abundancia de almejas de agua dulce del género* Epioblasma *en Norte América durante los últimos 5000 años. La abundancia relativa de Epioblasma declinó constantemente durante este período, lo que podría explicarse por el incremento de impactos humanos en los arroyos o por los cambios climáticos de largo plazo no relacionados con actividades humanas. Sin embargo, la tasa de declinación de* Epioblasma *aumentó significativamente después de la llegada de agricultura de maíz a gran escala en el sureste de Estados Unidos hace 1000 años aproximadamente. Nuestros resultados sugieren que las actividades humanas de uso de suelo en la prehistoria provocaron cambios en las comunidades de almejas de agua dulce que fueron menores en magnitud, pero similares en dirección, que los cambios causados por actividades recientes.*

Palabras Clave: diversidad de agua dulce, *Epioblasm,* impactos humanos prehistóricos

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Introduction

Freshwater ecosystems worldwide are beleaguered by the increasing demands of a growing human population. In the southeastern United States, a variety of pressures threaten highly diverse aquatic communities, including the richest freshwater mussel fauna (order Unionoida) on Earth (297 North American species, 269 in the southeastern United States; Neves et al. 1997). Historically, freshwater mussels have been highly sensitive to human-induced changes in aquatic habitats and today they represent the most endangered group of organisms in North America. At least 21 species have become extinct in the last 100 years (7% of the total fauna), and 194 (65%) are considered imperiled (Williams et al. 1993). Members of the genus *Epioblasma* have suffered a particularly severe decline. Of 20 recognized species, mostly endemic to the southeastern United States, 13 became extinct in the twentieth century, indicating that these species were especially intolerant of human-induced changes to rivers. Although localized mussel declines are often attributable to reservoir construction, stream channelization, or point-source pollution (Neves et al. 1997), the widespread nature of declines worldwide implies that other, large-scale disturbances associated with human land use, such as sedimentation and nonpoint-source pollution, have equally large impacts on these animals.

Beginning about 5000 years before present (BP), steady increases in the human population of the southeastern United States resulted in an increased rate of land clearance and disturbance that was associated with agriculture, acquisition of wood for fuel, game management, and other activities (Delcourt 1987; Johannessen 1993; Peacock 1998). These disturbances intensified coincident with the advent of large-scale maize agriculture beginning about 1000 BP (Lopinot 1992). The impact of these activities on water quality and aquatic organisms, including freshwater mussels, has not been examined.

Native Americans exploited freshwater mussels as food throughout the Holocene, and extensive shell deposits (middens) associated with human habitation sites occur along major rivers in the midwestern and south central United States. Because prehistoric humans likely harvested mussels indiscriminate of species (Matteson 1960; Peacock 2000), these data provide important records of prehistoric mussel assemblages and are used for reconstructing paleoenvironmental conditions (Morey & Crothers 1998) and establishing ranges of species that predated modern human impacts (Peacock & James 2002). Although few species extinctions or extirpations are documented in the archaeological record (Bogan 1990; but see Williams & Fradkin 1999), little is known about long-term prehistoric trends in mussel abundance and species composition. We used data from archaeological shell middens to examine prehistoric trends in the abundance of freshwater mussels of the genus *Epioblasma* in rivers in the southeastern United States during the last 5000 years. To assess potential impacts of changes in Native American land-use patterns on freshwater mussel communities, we examined differences in the rate of change of *Epioblasma* abundance before and after the advent of maize agriculture.

Methods

We compiled data from published and unpublished archaeological reports on mussel community composition from 41 temporally distinct prehistoric shell assemblages representing 27 sites and 12 rivers, mostly in the southeastern United States (Table 1). A complete list of data sources is available from the senior author. A variety of contexts, from general cultural layers to the fill of features (e.g., pits, postholes) are represented in these data sets. Assemblages were excluded if they appeared to be of mixed cultural origin (e.g., if pits intruded into earlier strata, mixing the shell), if an insufficient number of depositional contexts were represented (e.g., shell collected from the surface of a site), or if shell was recovered using nonstandardized methods (Peacock 2000). For samples without a specific date assigned only to a general cultural period, we used the midpoint of the reported cultural period as the date for that sample. We used the following cultural period definitions (BP): Late Archaic (5000–2500), Early Woodland (2500–2000), Middle Woodland (2000–1500), Late Woodland (1500–1000), and Mississippian (1000–500) (Steponaitis 1986). We did not include mussel assemblages assigned to "transitional periods."

We calculated the relative abundance of *Epioblasma* spp. as a percentage of total shells represented in each sample. We tested for relationships between time and relative abundance of *Epioblasma* in two ways. First, we conducted a randomized linear regression of relative abundance (as arc-sine transformed proportions) on time (10,000 randomizations; Manly 1997). We also fit curvilinear models to the data and, although significant, none were an improvement over the linear model. Second, we conducted a randomized Mantel test between two pair-wise distance matrices of differences in time and differences in relative abundance between samples (10,000 randomizations; Manly 1997).

To examine effects of changes in human land use on mussel communities, we calculated the rate of change (percent/100 years) in *Epioblasma* spp. relative abundance between pairs of temporally successive mussel assemblages found at the same site ($n = 13$ pairs). We grouped pairs of observations into two categories: before and after the advent of maize agriculture (1000 BP). We included pairs of observations that straddled this boundary in the "after-maize" category. We calculated the mean rate of change and percentile bootstrapped 95% confidence

Table 1. Prehistoric mussel assemblages from the eastern United States examined in this study.

River, State, County[a]	*Cultural period (sample size,%* Epioblasma*)*[b]	Epioblasma *spp. present*[c]
Clinch, TN, Roane	Woodland (20238, 13.7), Mississippian (2713, 17.8)	arc, bre, cap, flo, hay, obl, pro, ste, tor, tri
Cumberland, KY, Livingston	Mississippian (4913, 21.47; 1551, 7.22)	arc, fle, tor
Cumberland, TN, Davidson	Mississippian (4548, 18.6; 1642, 12.3)	arc, bre, cap, fle, flo, hay, pro, ste, tor
Cumberland, TN, Jackson	Archaic (12060, 12.6; 4548, 15.4)	arc, bre, fle, hay, obl, pro, tor, tri
Cumberland, TN, Smith	Woodland (715, 11.3)	arc, bre, cap, flo, hay, obl, ste, tor
Cumberland, TN, Smith	Woodland (827, 8.3)	arc, bre, cap, fle, flo, hay, lew, obl, ste, tor
Cumberland, TN, Davidson	Mississippian (762, 2.6)	arc, bre, hay, pro
Green, KY, Butler	Archaic (2215, 21.0; 2248, 18.0)	obl, per, pro, tor,[d] tri
Green, KY, Butler	Archaic (16279, 37.7)	tor, [d] tri
Hiwassee, TN, Bradley, McMinn	Mississippian (167, 1.2)	tor
Kentucky, KY, Woodford	Mississippian (>400,[e] 2.5)	sam, tor[d]
Little Pigeon, TN, Sevier	Mississippian (3855, 2.0)	bre, cap, flo, hay, ste, tor
Little Tennessee, TN, Monroe	Mississippian (707, 1.1)	bre, hay, lew, ste
Pond, KY, Hopkins	Mississippian (2162, 2.4)	tor,[d] tri
Scioto, OH, Ross	Woodland (1977, 21.4)	obl, tor, tri
Tennessee, AL, Lauderdale	Archaic (1185, 50.5), Woodland (830, 34.8)	arc, bie, bre, fle, flo, hay, lew, obl, per, pro, ste, tor
Tennessee, AL, Lauderdale	Archaic (10473, 28.1), Woodland (7451, 21.2)	arc, bie, bre, cap, fle, flo, hay, lew, obl, per, pro, ste, tor
Tennessee, AL, Jackson	Woodland (3148, 1.5)	arc, bre, fle, lew, pro, ste, tor, tri
Tennessee, TN, Meigs, Rhea	Woodland (945, 6.7; 11363, 6.2), Mississippian (2794, 1.0)	arc, bre, cap, fle, flo, hay, lew, obl, pro, ste, tor, tur
Tennessee, AL, Jackson	Archaic (1938, 9.4), Woodland (48196, 4.9)	arc, bie, bre, cap, fle, hay, lew, pro, ste, tor, tri
Tennessee, AL, Lauderdale	Archaic (2537, 22.0) Woodland (630, 12.7)	arc, bie, bre, cap, fle, flo, hay, lew, pro, ste, tor
Tennessee, AL, Lauderdale	Archaic (2980, 30.6)	arc, bie, bre, cap, flo, hay, lew, per, pro, ste, tor
Tennessee, TN, Loudon	Woodland (593, 19.1), Mississippian (931, 14.3; 9206, 14.3)	arc, bre, cap, hay, lew, pro, ste, tor, tri
Tombigbee, MS, Clay, Lowndes and AL, Pickens	Woodland (46801, 6.4) Mississippian (6911, 1.2)	pen
Wabash, IL, Crawford	Archaic (8135, 15.5)	obl, tor,[d] tri
Wabash, IL, Crawford	Archaic (6557, 30.6)	obl, tor,[d] tri
Wabash, IL, Lawrence	Archaic (18516, 15.2)	obl, tor,[d] tri

[a] *State abbreviations: TN, Tennessee; KY, Kentucky, OH, Ohio; AL, Alabama; MS, Mississippi; IL, Illinois.*

[b] *Sample size is the total number of shells (all species) present in each assemblage; assemblages with two different samples size entries indicate two temporally distinct samples within that cultural period.*

[c] *Species abbreviations: arc,* arcaeformis*; bie,* biemarginata*; bre,* brevidens*; cap,* capsaeformis*; fle,* flexuosa*; flo,* florentina*; hay,* haysiana*; lew,* lewisi*; obl,* obliquata*; pen,* penita*; per,* personata*; pro,* propinqua*; sam,* sampsoni*; ste,* stewardsoni*; tor,* torulosa*; tri,* triquetra*; tur,* turgidula.

[d] *Reported as* Epioblasma cincinnatiensis, E. phillipsi, or E. rangiana.

[e] *Exact sample size not given.*

intervals of *Epioblasma* relative abundance before and after maize. We tested for differences in the rates of change during these two time periods with a randomized one-way analysis of variance (10,000 randomizations; Manly 1997).

Results

Relative abundance of *Epioblasma* in mussel communities in the southeastern United States declined significantly from 5000 to 500 BP. Relative abundance was linearly and negatively related to time ($R^2 = 0.369$, $p < 0.0001$, Fig. 1), and distance matrices of time and relative abundance were significantly associated (Mantel $r = 0.142$, $p < 0.0004$). Although the slope of the linear relationship is low (0.0043; 95% CI, 0.0027–0.0061), over time this gradual decrease in abundance resulted in major changes in mussel community composition. Mean relative abundance of *Epioblasma* decreased from 23.6% (95% CI, 17.9–30.0) in the Archaic to 8.0% (4.4–11.9) in the Mississippian.

The rate of decline in the relative abundance of *Epioblasma* differed over time. Although we could fit both linear and curvilinear functions to the relationship between time and *Epioblasma* abundance, a conspicuous cluster of low values of *Epioblasma* abundance was evident after the advent of maize agriculture (Fig. 1). The mean rate of decline in *Epioblasma* abundance between paired, temporally successive samples was significantly higher after the advent of maize agriculture ($F_{1,11} = 5.07$,

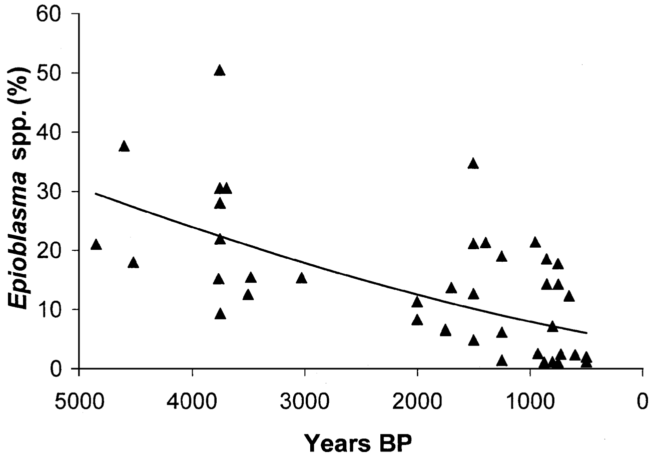

Figure 1. Relationship between time and relative abundance of Epioblasma *spp. in the eastern United States (arc sine [relative abundance] = 12.119 + 0.0043 time,* $R^2 = 0.369$, $p < 0.0001$*). The regression line was created using back-transformed predicted* y *values generated from the regression equation.*

$p < 0.017$; mean rate of decline/100 years [95% CI]: before maize = 1.38 [-0.79-3.01], $n = 7$; after maize = 14.81 [4.81-27.51], $n = 6$). The confidence interval around the mean decline before maize included zero, suggesting little or no decline during this time period. In contrast, the confidence interval after maize did not include zero but was wide, indicating high regional variation in the rate of decline.

Discussion

Although the climate of eastern North America changed continually throughout the Holocene, including small but abrupt temperature fluctuations during the last 1000 years (Gates 1993), the major climate changes occurred prior to 9000 BP (Webb et al. 1993). After the hypsithermal climatic optimum (6000 BP), distribution of vegetative communities has been similar to the present day (Delcourt & Delcourt 1987; Webb et al. 1993), suggesting a relatively stable climate during our study period. Nonetheless, we cannot discount the possibility that prehistoric declines in relative abundance of *Epioblasma* represent mussel community responses to long-term climatic changes and are unrelated to human effects on the landscape. Temporal variation in the rate of *Epioblasma* decline, however, is coincident with changes in prehistoric Native American land use. Together with the sensitivity of *Epioblasma* to recent anthropogenic stream alterations, prehistoric land-use patterns provide a compelling explanation for changes in abundance of these species seen over the last 5000 years.

Throughout the Late Archaic and Woodland periods (5000–1000 BP), prehistoric Americans gradually but steadily increased their dependence on a suite of native cultigens (the Eastern Agricultural Complex; Yarnell 1993). Concomitant increases in land clearing for cultivation of these crops resulted in conspicuous increases in the pollen record of disturbance-favored plants (e.g., ragweed, *Ambrosia* spp. L.; American cane, *Arundinaria gigantea* [Walt.] Muhl.) (Chapman et al. 1982; Delcourt 1987; Delcourt et al. 1998). During this period of gradual but steady increases in anthropogenic environmental disturbance, abundance of *Epioblasma* showed at most a gradual, low rate of decline.

About 1000 BP, most Native American groups in the southeastern United States adopted maize-based agriculture, supplemented by beans, squash, and continued cultivation of Eastern Agricultural Complex crops (Fritz 1990; Lopinot 1992). Adoption of maize occurred simultaneously with a rapid increase in the intensity and scale of agriculture throughout the Mississippian. Fields reaching tens to hundreds of hectares in size became a common feature across the landscape (Peacock 1998), and settlement hierarchies based on an agricultural surplus were established (Peebles 1978). During this time, indicators of anthropogenic disturbance such as charcoal influx and sedimentation rates increased markedly (Chapman et al. 1982), showing widespread intensification of land use and soil erosion (Steponaitis 1986; Delcourt 1987; Delcourt 1997). Similarly, the mean rate of decline in *Epioblasma* abundance increased sharply during this period of rapid intensification of anthropogenic disturbance and was an order of magnitude higher than before the advent of large-scale maize agriculture in the region.

Epioblasma declined even more dramatically in the twentieth century, relative to prehistoric declines, and these species are now extirpated from all our study sites or extinct (Neves et al. 1997). Although the causes of widespread, modern-day declines in mussel populations remain unclear, stream sedimentation associated with large-scale land disturbance is implicated as a primary cause (Bogan 1993). Our results from prehistory support the notion that increases in land clearance and disturbance have measurable effects on freshwater mussel communities. Further, our results suggest that prehistoric human populations exerted substantial pressures on aquatic ecosystems that were similar to, but less acute than, pressures exerted by modern-day society.

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