MASTODONS (*Mammut americanum*) AND THE LATE-GLACIAL VEGETATION OF THE EASTERN USA

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ABSTRACT

Numerous studies of tooth plaques and remains of gut contents of have confirmed that mastodon diet was composed of woody browse species, forbs, nuts, and fruits. However, fossil gut contents also suggest that mastodon diet included significant amounts of spruce, even though spruce is a low-quality, chemically-defended food. Most extant large mammals only browse on spruce when all other food sources are exhausted, and mastodon tusk growth increments indicate that mastodons were not food limited as they moved toward extinction (Fisher, 2009). Here we review the vegetation associated with mastodon habitat from the Great Lakes to the Gulf Coast, USA, over the period 18-10 ka cal BP using pollen assemblage data from 29 sites located near proboscidean fossil remains. Pollen data were acquired from the Neotoma Database and pollen abundance was converted into species biomass abundance using the Landscape Reconstruction Algorithm (LRA) of Sugita (2004a, 2004b). Although spruce was the dominant conifer throughout the Great Lakes Region until *ca*. 10 ka cal BP, deciduous species such as ash, oak, and elm comprised 50% or more of the vegetation assemblages even at the earliest and northernmost sites, and remained at similar levels until mastodon extinction. Many of these species have been found in mastodon gut contents. These vegetation assemblage reconstructions support the suggestion that mastodons were not food limited as they neared extinction. Moreover, these analyses of landscapes surrounding mastodon sites strongly suggest that the contemporaneous forest, composed of large amounts of spruce intermixed with ash, elm, and oak, was unlike the forests found in much of eastern North America today.

NOTE: ***In February, 2018, Daniel C. Fisher, Claude W. Hibbard Collegiate Professor of Paleontology and Director of the Museum of Paleontology, University of Michigan, gave an invited lecture at the University of Minnesota Duluth. In preparation for Dr. Fisher's visit, a seminar course was organized that focused on ecology, adaptation, and extinction of proboscideans. This poster is the final synthesis of that course. Six of the co-authors are students.***

Background

Occurrences of mastodon fossils and the associated vegetation has led to a wide range of speculation on dietary component of proboscideans. For example, Teale and Miller (2012) suggest that material interpreted to be gastrointestinal or fecal matter was mainly composed of spruce, possibly with minor amounts of pine, and that such a diet would have nutritionally stressed mastodons. Yansa and Adams (2012), in their study of proboscideans in the Great Lakes Region, suggest that American mastodons consumed primarily leaves and branches of spruce and other trees, and the vegetation transitioned from a spruce parkland / sedge assemblage to a spruce-dominated forest as the proboscideans neared extinction. Yansa and Adams (2012) speculate that mastodon populations declined as the dominant vegetation assemblage became a closed forest with a lesser amount of spruce trees, grasses, and sedges and an increase in the amount of deciduous trees. In contrast to the assertion of Yansa and Adams (2012) that forests became more closed, Jackson et al. (1986) in their study of the Kolarik Mastodon Site, suggest that during the Late Glacial Indiana was an open spruce parkland similar to northern Quebec and Labrador today. The abundance of conifer needles and cone scales in the gut contents of mastodon remains may provide a significant look into mastodon foraging strategies, particularly late in winter. The needles may well be incidental and the primary target of the proboscidean may have been cone bundles, which would have contained a high-quality nutritional supplement. Other components of the Late Glacial floristic assemblage may also have been important nutritionally; McAndrews (2003) emphasizes that shrubby cinquefoil (*Potentilla palustris*), a sprawling boreal to temperate shrub, would have been a prime browsing target. Twigs of other deciduous species have been found in mastodon gut contents (Lepper et al. 1991).

Methods

To examine floristic assemblages of mastodon habitat from the Great Lakes to the Gulf Coast, we compiled pollen assemblage data from 29 sites that are located near proboscidean fossil sites from the Gulf Coast to the Great Lakes Region. Although pollen diagrams record species present at the site, the degree to which pollen abundance represents species abundance has been the focus of numerous studies (e.g. Davis, 1960; Webb, 1974; Calcote, 1995; Sugita, 1994, 2004a, 2004b).

Interpretation of the compositional structure of Late Glacial vegetation assemblages, and therefore mastodon habitat, is complicated by the lack of modern analogs (Gill et al., 2012). Wright (1968) and Davis (1981), were among the earliest to show that that boreal species in the Late Glacial were part of a vegetation assemblage far different from the modern boreal forest. The vegetation assemblage was characterized by low abundances of typical boreal species and high abundances of deciduous species such as oak, ash, elm, hornbeam/ironwood. In addition to the lack of analogs, the degree to which pollen abundance represents species abundance is the focus of great debate. Because of the lack of modern analogs for the Late Glacial vegetation communities, we employed the Landscape Reconstruction Algorithm (LRA) of Sugita (2007a, 2007b), to evaluate the relative abundance and diversity of species on the Late Glacial landscape. Pollen abundance in sediment cores depends on the relative production of pollen of different species and on preservation. However, relative abundance is also strongly influenced by basin size (Sugita, 2007a). For evaluation of proboscidean habitat, we are interested in the relative abundance of vegetation at the landscape at a scale of 104 – 105 km2. Pollen samples from "large lakes" exhibit little site-to-site variation even if the regional vegetation is highly heterogeneous and therefore represents the regional abundances (Sugita, 2007a). Smaller basins, on the other hand, can have large site-to-site variability resulting from local factors like differential pollen productivity and dispersal distance, proximity to sources, mixing, etc. (Sugita, 2007a). Therefore, there are definable relationships among sedimentary basin size, species abundance, relative pollen productivity, and pollen dispersal characteristics.

The Landscape Reconstruction Algorithm

In simple form, the pollen loading of a species on the surface of a sedimentary basin is a function of pollen productivity of the species and the spatial integral of mean plant abundance, distribution of the species on the landscape, and pollen dispersal characteristics. Over an area within 100 to 400 km radius of a sedimentary basin, the relation between pollen load and species abundance is expressed as

$$y_{i,k} = P_i \cdot \int_R^{Z_{max}} \overline{X}_i \cdot g_i(z) \cdot \mathrm{d}z$$

where $y_{i,k}$ is pollen loading of species i on basin k, P_i is pollen productivity of species i per unit area, R is radius of the sedimentary basin, Z_{max} is the distance over which the pollen originates, X_i is mean abundance of species i within Z_{max}, z is distance from the sedimentary basin, and $g_i(z)$ is the dispersal and deposition function of pollen for species i (we refer readers to Sugita, 2004a,2004b for the details of the LRA). The LRA consists of two parts. First, REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) is used to get the regional vegetation abundances. Once the regional abundances are estimated, LOVE (LOcal Vegetation Estimates) can be estimated by subtracting the regional signal. For the purposes of this investigation, we are interested in the regional vegetation assemblage and therefore utilize REVEALS. A number of factors are required to run REVEALS such as radius of the sedimentary basin, the length scale of the landscape, and relative pollen productivity estimates.

Pollen Productivity Estimates (PPE) – Numerous studies have addressed the relative production and preservation of pollen in sediment cores (*e.g.* Calcote, 1995; Brostrom et al., 2004; Stedingk et al., 2008, Chaput and Gajewski, 2018, among others). We compiled existing PPEs and calculated settling velocities (Table 1) for 28 species from the wide variety of studies presented in literature. All values are normalized to *Poaceae*.

Table 1. Pollen Productivity Estimates.

Taxon	Fall speed	α-Mean
Acer rubrum	0.056	1.1
Acer saccarum	0.056	0.8
Alnus	0.021	6.6
Artemisia	0.021	3.1
Betula	0.024	6.6
Calluna	0.042	1.1
Cerealia	0.060	1.1
Chenopodiaceae	0.021	4.3
Corylus	0.025	1.2
Cyperaceae	0.035	1.4
Fagus	0.057	6.7
Fraxinus	0.022	0.8
Gramineae	0.035	1.0
Picea	0.056	5.0
Pinus	0.031	8.1
Plantago	0.027	3.7
Poaceae	0.035	1.0
Populus	0.027	0.4
Potentilla	0.035	4.2
Quercus	0.035	5.6
Rumex	0.022	1.6
Salix	0.022	1.3
Sambucus	0.014	1.3
Tilia	0.032	0.9
Tsuga	0.071	3.4
Ulmus	0.032	1.3
Urtica	0.007	10.5

Table 2. Study Area Sites and Locations. A total of 13 pollen cores were selected for detailed study.

Pollen Sites		Longitude	Latitude
Michigan			
Demont Lake		-85.0543	43.5079
Vestaburg Bog		-84.8942	43.3909
Indiana			
Pinhook Bog		-86.5446	41.6385
Spicer Lake		-86.5466	41.7149
Clear Lake		-86.8467	41.6150
Hudson Lake		-86.5221	41.7574
Southern Appalachians			
Anderson Pond		-85.5013	36.0302
Pigeon Marsh		-85.4013	34.6636
Quicksand Pond		-84.8653	34.3264
Cahaba Pond		-86.5333	33.5000
Gulf Coast			
Goshen Springs		-86.1342	31.7211
Camel Lake		-85.0167	30.2667
Lake Louise		-83.2583	30.7250

Study Areas

Four regions with fossil evidence of mastodons and with pollen records that span the interval from 18ka to 10ka were chosen from our 29 identified sites to evaluate regional vegetation abundances: (1) central Michigan, which was near the margin of the Laurentide Ice Sheet during the Late Glacial; (2) northern Indiana; (3) the southern Appalachians in Tennessee, Alabama, and Georgia; and (4) along the Gulf Coast in Florida, southern Alabama, and southern Georgia. Within each region, pollen cores from lakes nearest several proboscidean death sites were chosen for further analyses of contemporaneous vegetation (Figure 1, Table 2). For each site the basin size was estimated as a function of time because most of the lakes have undergone considerable decrease in size from closure by encroachment of floating vegetation mats. PPEs, fall velocity, basin size, and the special scale of each area were input into the LRA and the simulations were run.

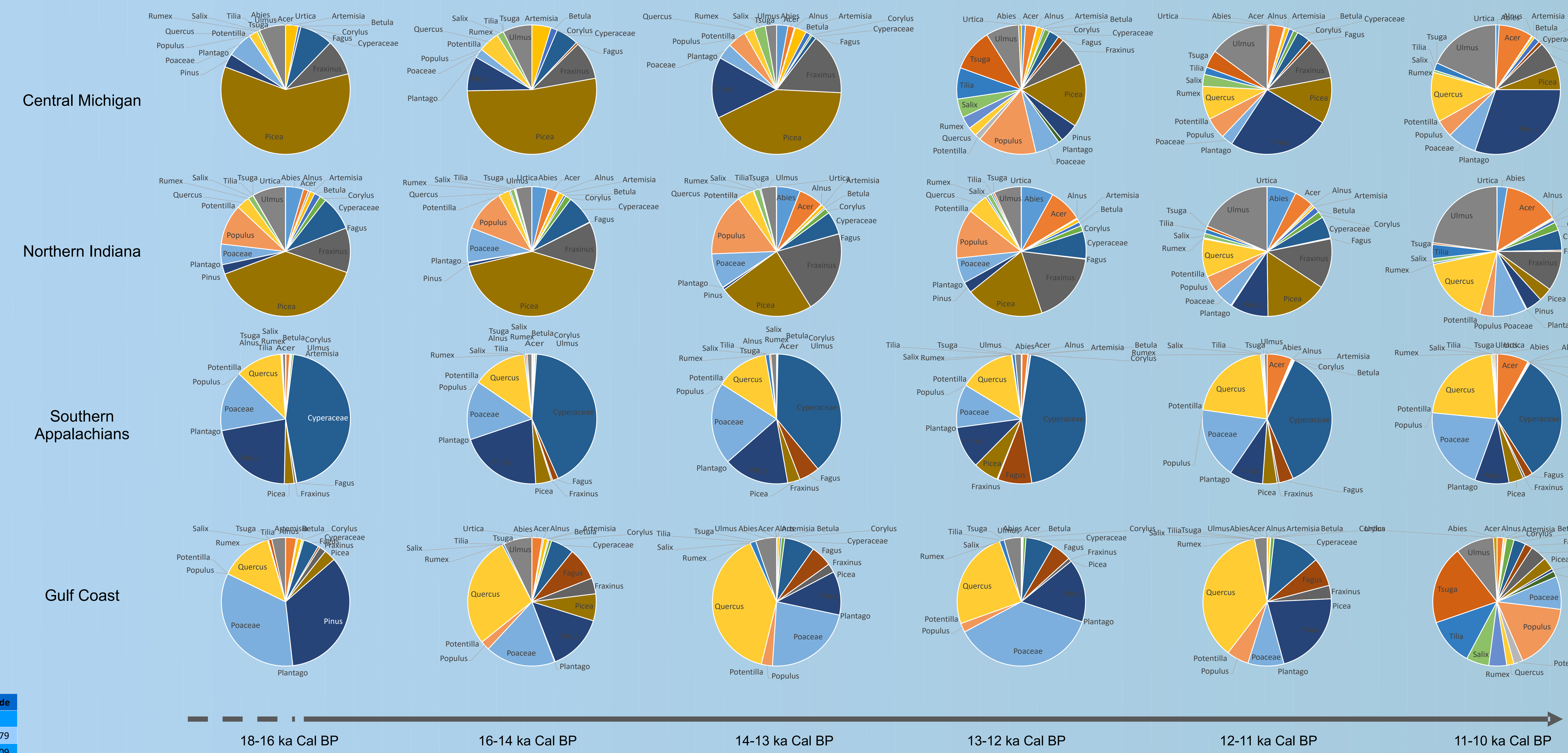
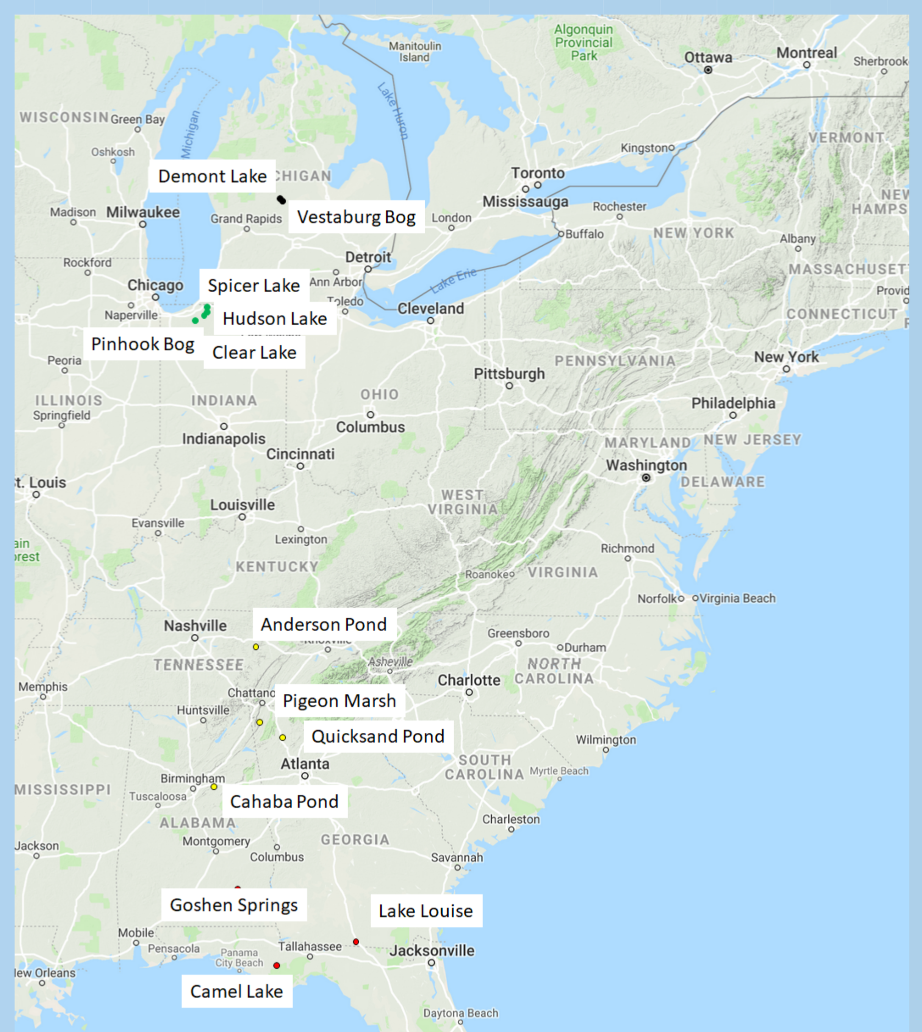


Figure 2. Results of the Landscape Reconstruction Algorithm. Reconstructions were compiles for 1000 year intervals from 10 ka to 14 ka and then in 2000 year intervals for the period 14-16 ka and 16-18 ka Cal BP.

Results

The percentage cover of each species on the regional scale (10^4 – 10^5 km^2)were extracted for each specified time interval using output from REVEALS. We ran the simulations for the period 18ka to 10ka. An example of the output for northern Indiana is shown in Table 3. Vegetation abundances for all sites are plotted in Figure 2.

Figure 1. Location of Study Sites.



Summary

Spruce is a major component of the regional vegetation only at the northern sites, although it is present in lesser quantities in the southern Appalachians and Gulf Coast from 14-18 ka cal BP. Deciduous species such as oak, birch, aspen, elm, ash, and basswood, and presumably the typical shrubby understory that would accompany this forest assemblage, dominates the southern sites as might be expected at these lower latitudes. However, what is surprising is at the northern sites in northern Indiana and central Michigan, even during the period from 14-18 ka cal BP, deciduous species (as listed above with their herbaceous understory) represent approximately 50% of the vegetation on the landscape. The calculated vegetation abundances suggest that proboscideans of the Great Lakes region, even in the proximity of the ice margin near the Last Glacial Maximum, had abundant deciduous woody and herbaceous browse. In addition, in terms of proboscidean habitat, these results suggest that the quality of the diet potentially available to mastodons could have improved as mastodons neared extinction. The question this raises is why gut contents recovered from mastodons would not have indicated dietary changes to consume a higher quality food source.

These vegetation assemblage reconstructions support the suggestion that mastodons were not food limited as they neared extinction. Moreover, these analyses of landscapes surrounding mastodon sites strongly suggest that the contemporaneous forest, composed of large amounts of spruce intermixed with ash, elm, and oak, was unlike that found in much of eastern North America today .

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