RECONSTRUCTING EQUID MOBILITY IN MIOCENE FLORIDA

Wallace, Jenelle[1]; Crowley, Brooke E.[1,2]; Miller, Joshua H.[1]
[1]Department of Geology, University of Cincinnati, OH 45221
[2]Department of Anthropology, University of Cincinnati
Contact: walla2je@mail.uc.edu

Introduction

The Miocene Epoch was characterized by progressive cooling, aridification, and the expansion of grasslands. With increased grasses came the radiation of large-bodied grazers, such as horses. Equids reached their maximum diversity during the middle Miocene. Dietary adaptations diversified, body sizes generally increased, limbs lengthened, and toe numbers were reduced, presumably to accommodate the increasingly open landscape and consumption of grasses. How these environmental and morphological changes impacted equid mobility has not been explored. We used strontium isotope ratios ($^{87}Sr/^{86}Sr$) to reconstruct the mobility of horses that lived in northern Florida ca. 18 and 9 million years ago (Fig. 1).

Study Area

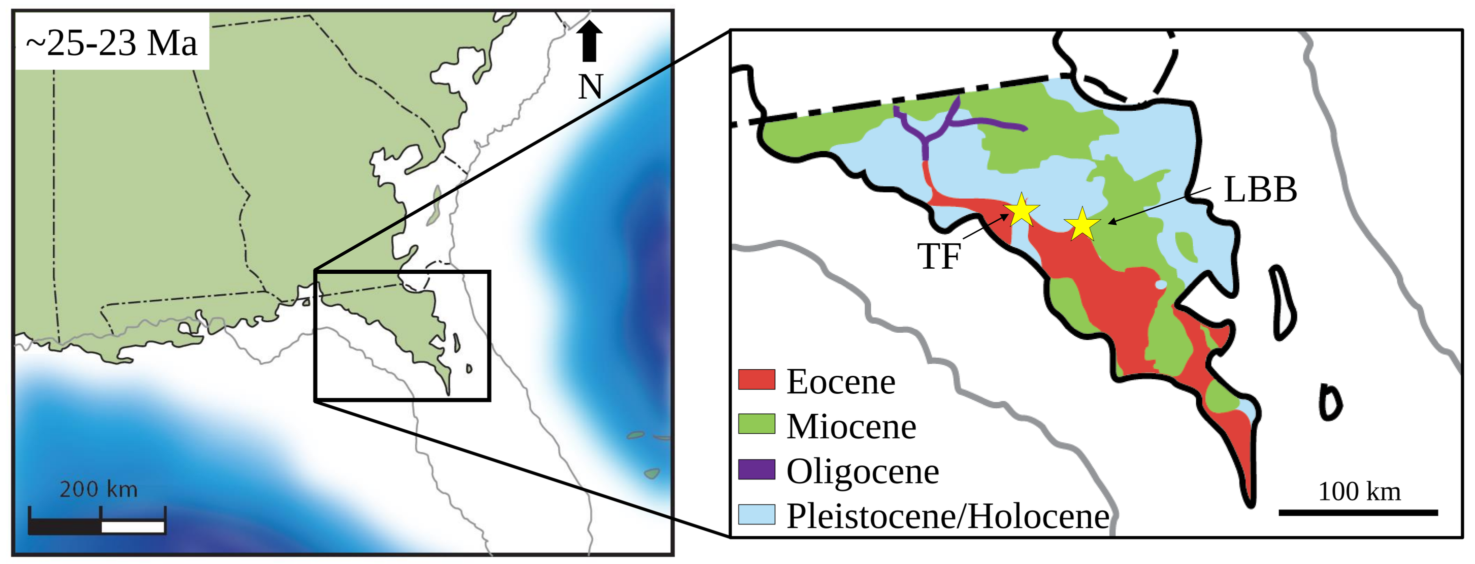


Figure 1. Paleogeographic map of the southeastern USA during the early Miocene (modified from Blakey 2017). The second panel illustrates modern sedimentary/carbonate bedrock geology in Northern Florida (modified from Scott et al. 2001). Miocene fossil sites are represented by two stars (TF= Thomas Farm, 18 Ma; LBB= Love Bone Bed, 9 Ma). Both sites are underlain by Eocene limestone and sit ca. 47 km apart.

Background on Sr Isotopes

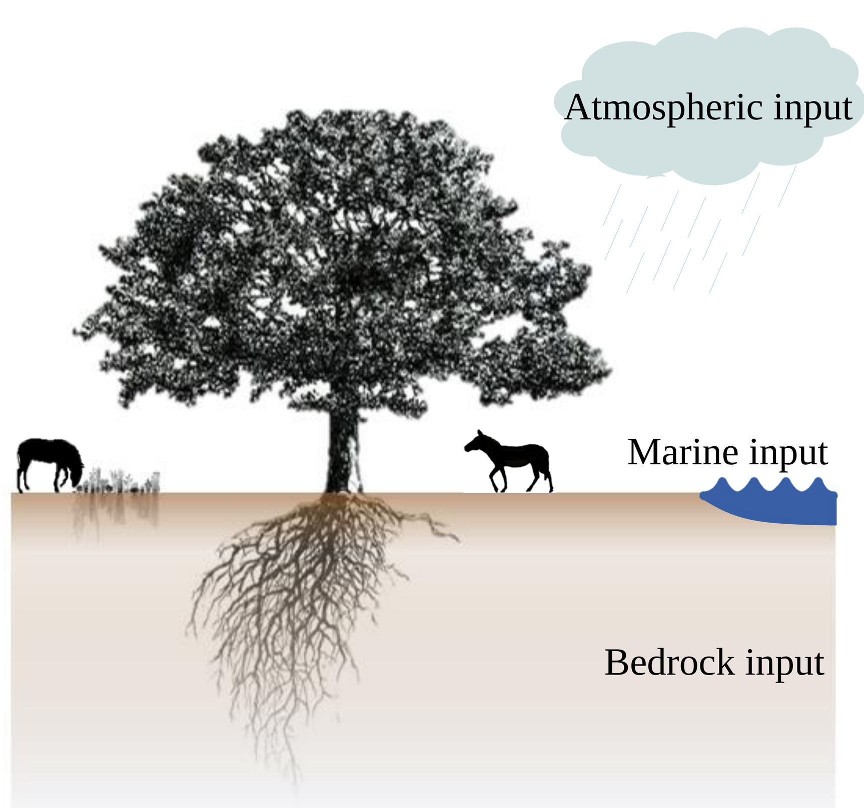
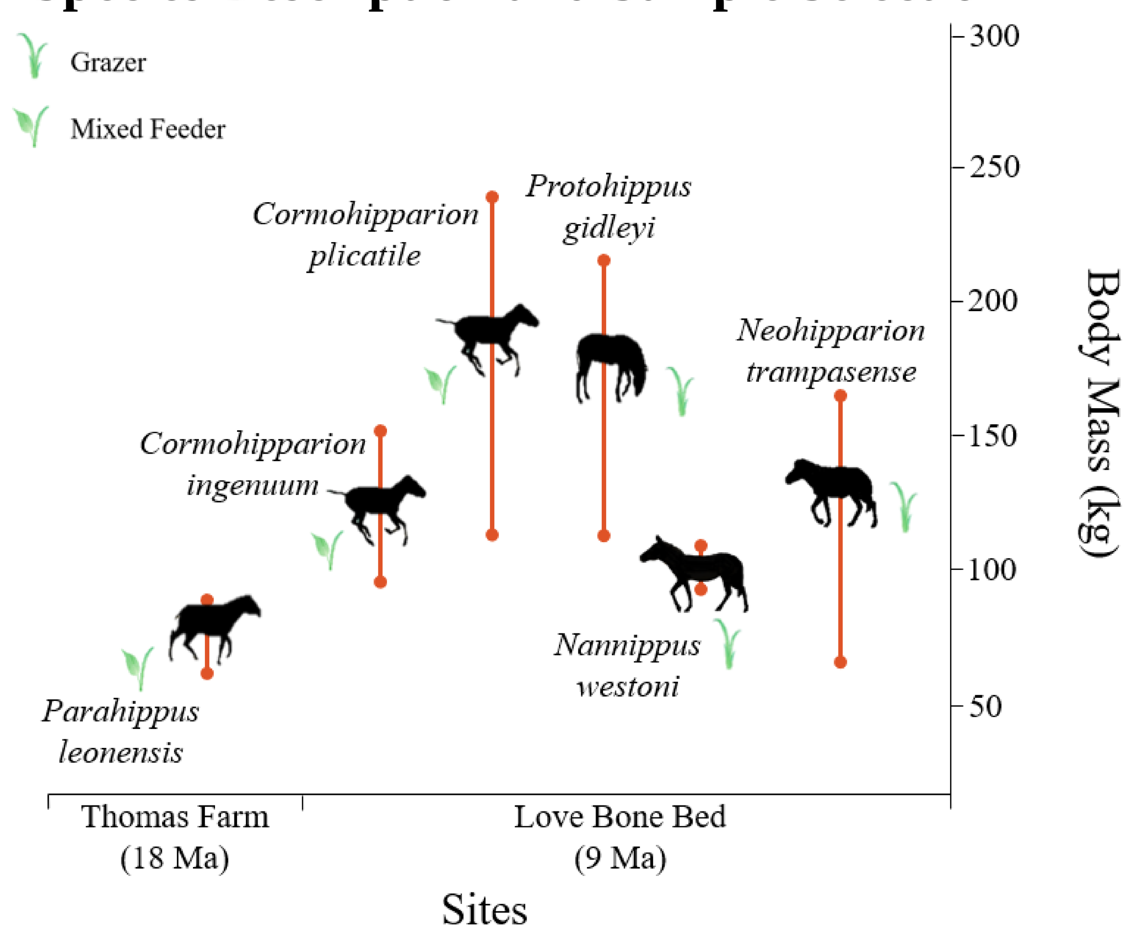


Figure 2. Diagram outlining possible strontium sources within an ecosystem. Whereas deeper rooted trees and shrubs likely obtain the majority of their strontium from underlying bedrock, shallow rooting grasses and herbs may be more strongly influenced by atmospheric sources (e.g. precipitation, sea spray, aerosols; Capo et al. 1998; USDA 2017).

Strontium isotope ratios primarily vary with bedrock geology and are thus dependent on the age and composition of underlying bedrock. However, there can also be atmospheric input via dust or aerosols, both wet and dry deposited (Fig. 2). Strontium isotopes can be used to track mammal mobility (Capo et al. 1998; Hoppe et al. 1999). Plants uptake strontium from weathering bedrock and atmospheric deposition (Fig. 2), and herbivores incorporate ingested strontium into their tooth enamel. Once teeth mineralize, $^{87}Sr/^{86}Sr$ is inert, and it is thus possible to track the mobility history of individuals (Capo et al. 1998).

Due to elevated sea levels during the Miocene, highly mobile individuals would have only been able to travel north towards the Appalachians (Fig. 1). Accordingly, Sr isotope ratios for relatively sedentary horses should resemble local Florida limestone, whereas highly mobile individuals are expected to have more variable $^{87}Sr/^{86}Sr$, reflecting foraging across a range of geologies further north. We expected that small equids and browsers would have the lowest and least variable $^{87}Sr/^{86}Sr$, indicating local movement. Larger-bodied species and grazers should have higher and more variable $^{87}Sr/^{86}Sr$, reflecting greater mobility.

Species Description and Sample Selection



We analyzed third molars from 49 individuals: one species from Thomas Farm (18 Ma) and five species from the Love Bone Bed (9 Ma). We selected species that were abundant, well-studied, and had a diverse range of body size and dietary adaptations (Fig. 3).

Figure 3. Reconstructed body masses and dietary adaptations for equids. Masses were estimated using M_1 length and width (data from MacFadden 1986, 1992). Red bars represent minimum and maximum estimates.

Sample Processing and Analysis

Roughly 20 mg of enamel were drilled from each tooth. Bulk samples were taken from the crown to the root of each tooth to account for variations of Sr throughout tooth mineralization (Fig. 4). Enamel was then pretreated with 30% H_2O_2 and 1 M acetic acid buffered with calcium acetate to remove organics and inorganic impurities. Sr isotopes were analyzed using a mullticollector ICPMS at the University of Illinois Urbana-Champaign. Nonparametric Wilcoxon and Kruskal-Wallis tests were used to evaluate differences in Sr distributions among sites and taxa.

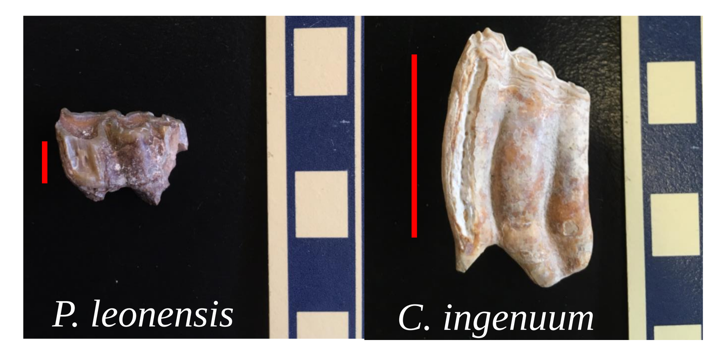


Figure 4. Photographs of sampled teeth illustrating our bulk enamel sampling strategy. Red bars indicate the sample area length. Scale is cm.

Results

Parahippus from Thomas Farm, which is the smallest equid included in our study, has lower $^{87}Sr/^{86}Sr$ than any equids from the Love Bone Bed (Fig. 5; χ^2=20.85; df=1; P<0.0001). Within the Love Bone Bed there are no significant differences among taxa (χ^2=6.11; df=4; P=0.1908). Overall, the data are fairly isotopically homogenous and there is little influence of diet and body mass. However, there are three outliers, two of which have significantly low $^{87}Sr/^{86}Sr$ (Fig. 5). We discuss these further in the Initial Interpretations section.

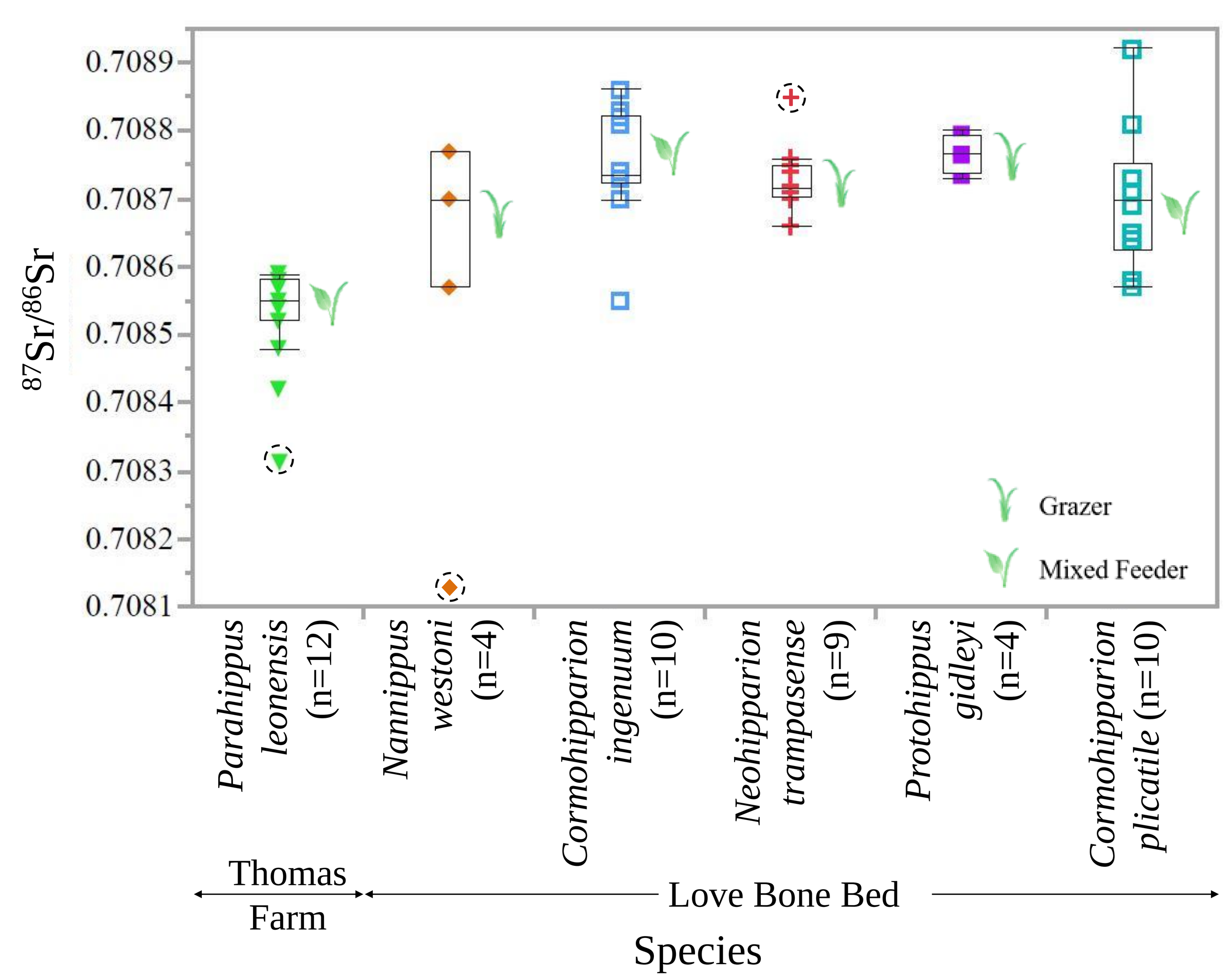


Figure 5. $^{87}Sr/^{86}Sr$ for equids at Thomas Farm and Love Bone Bed are sorted by increasing body mass (left to right). Dashed circles represent outliers and the box and whisker interquartile range indicate the 75th and 95th percentiles.

Initial Interpretations

Comparing $^{87}Sr/^{86}Sr$ for Miocene horses to Pleistocene and modern biota from the same region (Fig. 6), we see that modern and Pleistocene data are higher and more variable than Miocene horses. This suggests that Florida received less exogenous dust in the Miocene. Furthermore, comparing all biological data with those expected for local bedrock, and contemporaneous seawater, we note that all plot closer to contemporaneous seawater than bedrock, which implies that there has been a substantial marine influence on bioavailable Sr in northern Florida over time. We envision two potential scenarios can explain our results:

(1) The close match between estimated $^{87}Sr/^{86}Sr$ for Miocene seawater and measured $^{87}Sr/^{86}Sr$ for most equids (Fig. 6) suggests that most individuals regularly foraged close to the coast. The two outliers with lower $^{87}Sr/^{86}Sr$ more closely resemble bedrock geology and may have been relatively sedentary, remaining close to the fossil localities.

(2) Alternately, Thomas Farm and Love Bone Bed could have been much closer to coastal influence than they are today and marine-derived Sr may have been brought inland via wind or precipitation (Evans et al. 2010). In this scenario, lower $^{87}Sr/^{86}Sr$ would reflect foraging further from the coast.

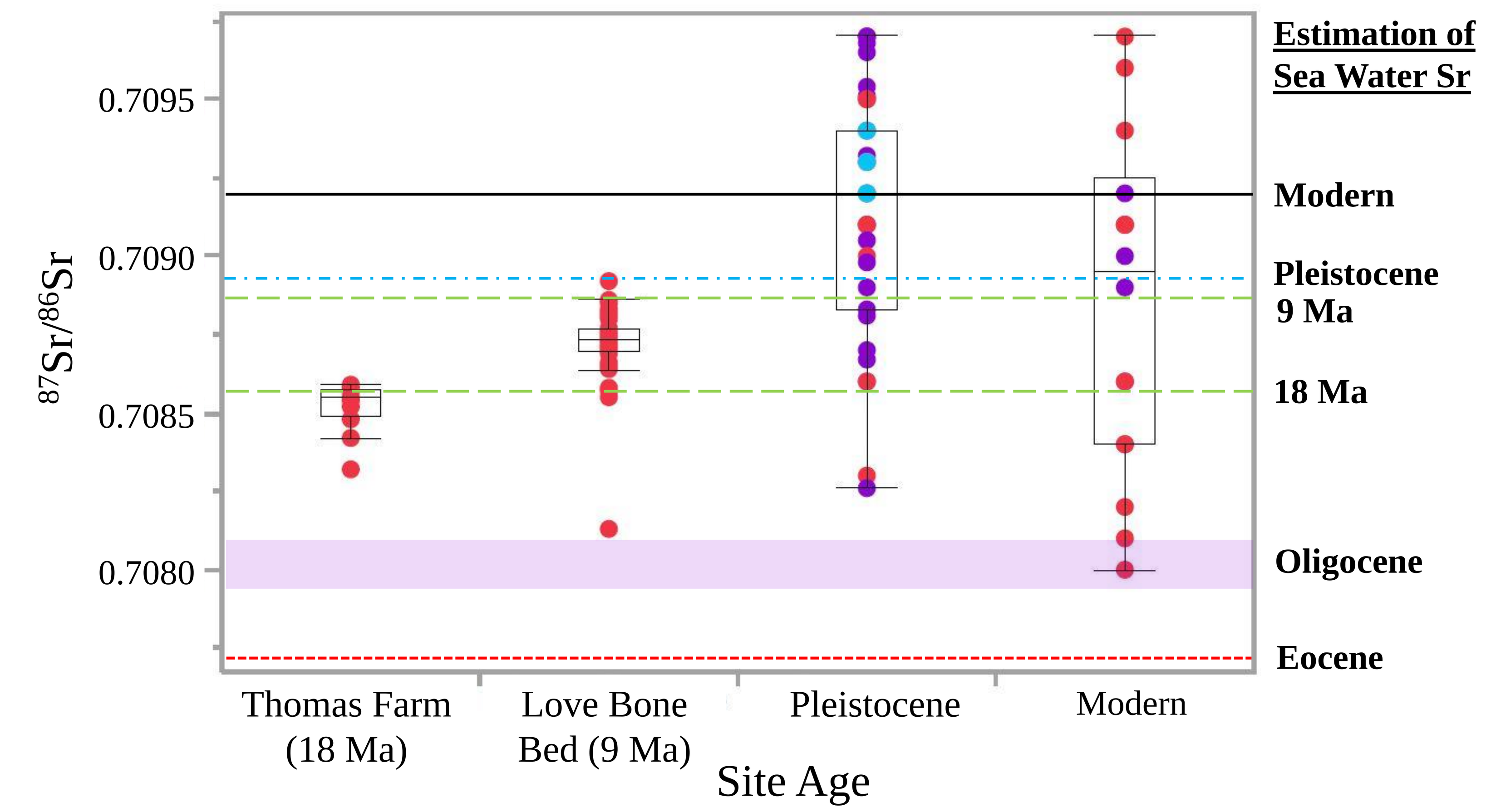


Figure 6. Boxplots showing $^{87}Sr/^{86}Sr$ for Miocene horses, Pleistocene mammals (Hoppe & Koch 2007), and modern plant and water samples from northern Florida (Hoppe et al. 1999). Horizontal lines represent estimated Sr isotope ratios of sea water during different periods (Koepnick et al. 1985). Colors correspond with geologies in Fig. 1.

Future Directions

This is the first study to examine mobility of terrestrial mammals prior to the Pleistocene, and the first to address spatial partitioning among contemporaneous equids with differing body masses and diets. While our results suggest that Miocene equids were less mobile than we had initially expected, the data do identify some individuals that may have been more mobile than the majority. It is generally accepted that bedrock dominates biologically available $^{87}Sr/^{86}Sr$, particularly where limestone is present (Capo et al. 1998). However, this does not explain Sr data from Northern Florida. Studies that disentangle the influence of multiple Sr sources are limited to arid settings, temperate forests, or windward coastal areas. More studies that examine the influence of atmospheric versus geologic sources on bioavailable Sr in leeward and coastal regions would be valuable.

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