# Discussion

## On the Environment of Aramis

### A Comment on White in Domínguez-Rodrigo

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Tim D. White incorrectly represents our work and the use of stable isotopes to understand Aramis paleoenvironments (Domínguez-Rodrigo 2014, comment by Tim D. White). He states that Cerling and colleagues (2010, 2011) "parsed *Ardipithecus* habitat as grassland rather than a mosaic spanning grassy woodlands to wooded grassland" (Domínguez-Rodrigo 2014, comment by White, 75). However, Cerling et al. (2010) wrote, "we find the environmental context of *Ardipithecus ramidus* at Aramis to be represented by what is commonly referred to as tree- or bush-savanna, with 25% or less woody canopy cover. The habitats involved probably ranged from riparian forest to grassland," and further, "if woodland or closed forest habitat was indeed present, . . . [it] might be found in a riparian corridor bordered by mixed and more open environments, including woody grasslands with < 25% canopy cover." And yet further, "Evidence from Aramis and elsewhere clearly shows that open savanna grassland was not the environmental context of *Ardipithecus*." None of these statements parses the *Ardipithecus* habitat "as grassland."

White claims that our "assertion that Aramis paleosol carbonates indicate only 5%–25% woody cover is invalid because their regression was anchored by non-African forest endpoints, biasing their woody-cover estimates significantly toward the open side. An alternative application of the same method and comparative data using only their 'East African' data set produces an Aramis range of 9%–78% cover" (Domínguez-Rodrigo 2014, comment by White, 75 n. 6). We are puzzled that White would compare a total range of values, including a > 4 sigma outlier, with that of a 1-sigma distribution about a mean value. Figure 1 shows the cumulative probability distribution of woody cover from Aramis (WoldeGabriel et al. 2009). These distributions are based on Cerling et al. (2011) using (1) data on all tropical and subtropical soils ($N = 76$), (2) data excluding tropical forests outside of Africa ($N = 67$), (3) data from Africa only ($N = 36$), and (4) data from East Africa only ($N = 28$). Estimates of woody cover for Aramis yield averages with 1-sigma distributions of 17 ± 9%, 17 ± 9%, 22 ± 10%, and 25 ± 10%, respectively. Thus, all methods indicate the dominant biome was "wooded grassland" using the White (1983) classification for African vegetation. For comparison, median percent woody cover at Kanapoi and Kanjera calculated using method 1 are ca. 50% and < 10%, respectively, indicating wood/bush/shrubland and grassland, respectively (fig. 1).

White (Domínguez-Rodrigo 2014, comment by White, 75 n. 6) states, "isotope values among the Aramis colobine specimens analyzed show the presence of closed canopy forest patches," but only 2 of 20 analyses indicate such conditions (i.e., $\delta^{13}C < -14‰$). *Kuseracolobus*, *Pliopapio*, and *Ardipithecus* have average $\delta^{13}C$ values of −12.6 ± 1.6 ($N = 20$), −10.9 ± 0.7 ($N = 14$), and −10.3 ± 0.9 ($N = 7$), respectively. All values for *Pliopapio* and *Ardipithecus* fall far outside the range suggestive of closed canopy; furthermore, White et al. (2009) suggest that all *Ardipithecus* individuals sampled for isotopes at Aramis had $C_4$-based resources as part of their diet (9%–28%). Thus, although closed canopy conditions may have been present at Aramis, isotopic arguments cannot be used to say that *Ardipithecus* used them.

White and colleagues (WoldeGabriel et al. 2009) say "the Aramis and adjacent drainage basins expose . . . 300 m of sediments largely deposited in rivers and lakes, and on floodplains, between 5.5 and 3.8 Ma. Within this succession, the *Ar. ramidus*–bearing rock unit comprises silt and clay beds deposited on a floodplain," an interpretation also preferred independently by Gani and Gani (2011), who also found strong evidence of fluvial sedimentation and suggested the presence of riparian environments. This agrees with Cerling et al. (2010), who suggested "a riparian corridor bordered by mixed and more open environments, including woody grasslands with < 25% canopy cover." However, White et al. (2010) say that "expected sedimentological, taxonomic, and taphonomic evidence for such settings is absent at the hominid-bearing fossil localities at Aramis." Astonishingly, White and colleagues (Ambrose et al. 2011) state that "geological and paleontological evidence for fluviatile deposition and riparian habitats is absent at Aramis," flatly contradicting their earlier description quoted above. We stand by our original interpretation of the isotopic evidence for Aramis biomes—limited closed canopy likely associated with riparian habitats, with extensive wooded grasslands and some true grasslands.

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Cerling, Thure E., Naomi E. Levin, Jay Quade, Jonathan G. Wynn, David L.

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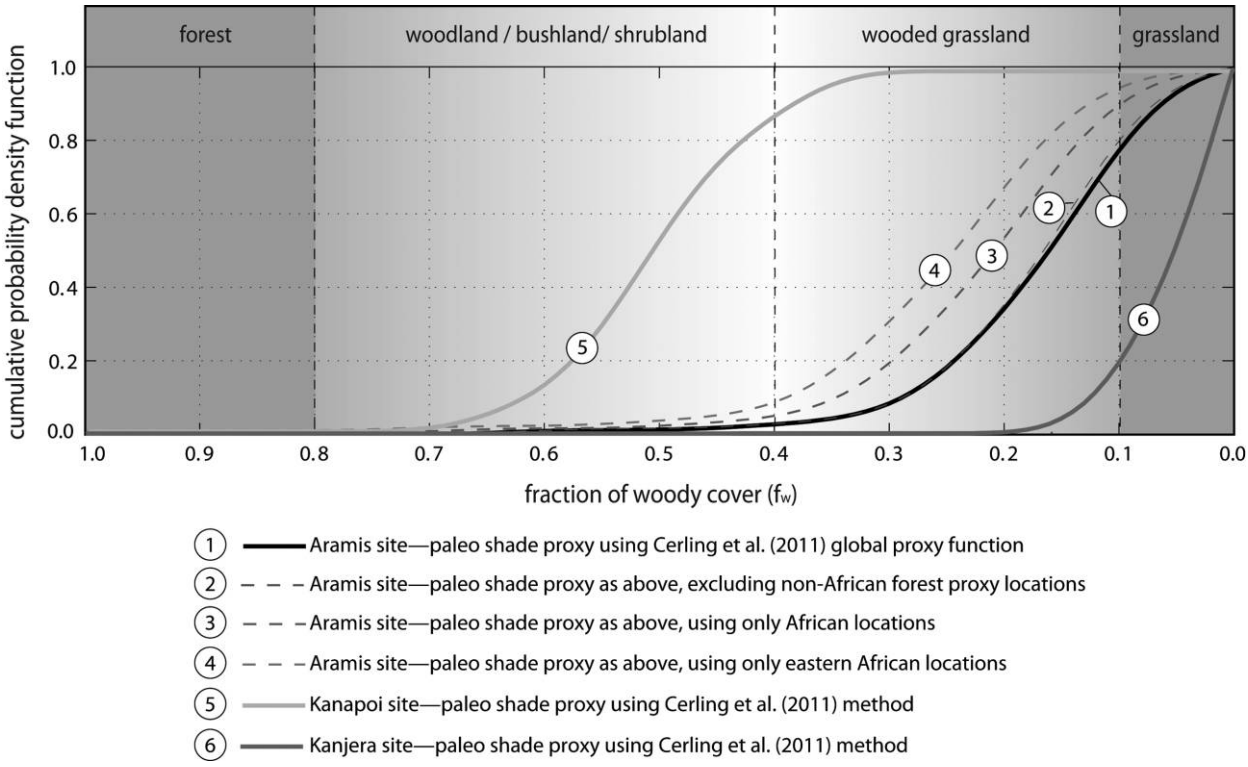


Figure 1. Cumulative probabilities of woody cover for Aramis, based on 85 paleosol analyses (data from WoldeGabriel et al. 2009). Only one of 85 samples has woody cover > 0.6, using any method of calculation. For comparison woody cover is shown for Kanapoi (Wynn 2000) and Kanjera (Plummer et al. 2009). A color version of this figure is available online.

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