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Steps of The Asian Giants: Modeling the body size related foraging ecology of *Meganthropus palaeojavanicus*, a 8 feet hominid in Central Java

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Abstract. *Meganthropus palaeojavanicus* was known very tall with body height of 8 feet and this made *M. palaeojavanicus* as the tallest hominid ever existed. This species was living in closed tropical woodland and hilly landscape as the fossil remains were found in a remote forest in Sangiran, central Java. Owing large body size, it may influence the foraging ecology of *M. palaeojavanicus* to cope with the terrain. In here, this study aimed to model the *M. palaeojavanicus* foraging ecology along terrain gradients. The model indicates that within 5 km home range radius, the most suitable foraging areas were in north east since these areas have more flat landscapes with slopes of <7.5%. While less suitable areas in north west and south west areas were characterized by hilly landscapes with rugged terrain and steep slopes with slopes of >62.8%.

Introduction

Java island is one of locations in South East Asia known for its prehistoric hominid presences. Von Koenigswald (1935) and followed by de Vos et al. (1985) and de Vos (1995) have reconstructed the faunal succession scheme of the Pleistocene of Java. In this island, the prehistoric faunas can be classified into three major units according the time periods. First was the oldest unit consisted of endemic and unbalanced fauna and this without hominid presences. After that, was the middle unit characterized by partially endemic Stegodon and *Homo erectus*. The younger period unit at late Pleistocene included balanced, non-endemic tropical rainforest fauna along with the presence of the earliest modern humans known as *H. sapiens* (van den Bergh et al. 2001).

Hominids in Java island represented a large spatio-temporal diversity. The first hominid was based on fossil found in Java in 1888 from Wajak cave in East Java. Later this hominid was assigned to *Homo wajakensis*. In central Java, Sangiran was known for its vast fossil presences representing various taxa (Widianto and Grimaud-Hervé 2014). In 2016, cranium of *Homo erectus* was found in Bojong creek (Figure 1) near Sangiran. Based on the analysis of several mandibles collected from Cemoro river in Sangiran, those hominids were classified into *Meganthropus palaeojavanicus*, *Pithecanthropus mojokertensis*, *P. dubius* and *P. robustus* and estimated from Lower to Middle Pleistocene (1.6 Ma - 0.1 Ma or less).

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Figure 1. Bojong creek (left) and Cemoro river (right) where fossils were found in Sangiran, central Java.

One of apparent taxa was the *Meganthropus palaeojavanicus*. At first, *Meganthropus* was classified as giant based on teeth and jaw fragments (Garn and Lewis) . Later on, Weidenreich (1945) determined that *Meganthropus* tooth-jaw fossils were belonging to group classified as extraordinarily large men of early Sino-Malaysian Fauna. Different from other hominids of Sangiran, this species was estimated very tall with body height of 2.44 m and weighed around 181 – 272 kg. Zanolli et al. (2019) have confirmed the presence of *Meganthropus* as a Pleistocene Indonesian hominid distinct from *Pongo*, *Gigantopithecus* and *Homo*. *Meganthropus* was more taller in comparison to other Asian hominids (Pope 1983). As a comparison, *H. erectus* height was within the range of 1.46-1.85 m shorter than *Meganthropus*. Localities of *Meganthropus* in Sangiran were characterized by forest and hilly landscapes. Given by the body size of *Meganthropus* and how this size can cope the particular landscapes, an understanding of the terrain effects on *Meganthropus* foraging patterns is relevant as to how variations in landscape influenced *Meganthropus* biogeography.

Methods

Study area

The study area was in the Sangiran landscape of central Java with areas of 262.45 km^2. This landscape bordered by 68.71 m Bengawan Solo river in east and connected with 20.29 Cemoro river in middle. This creek was crossing the landscape in the middle from West to East (Figure 2).

Landscape analysis

The Sangiran landscape was analyzed based on forest covers and contour line analysis. The forest cover was based on the interpretation of satellite imagery provided by Copernicus Land Monitoring Service (Buchhorn et al. 2020).

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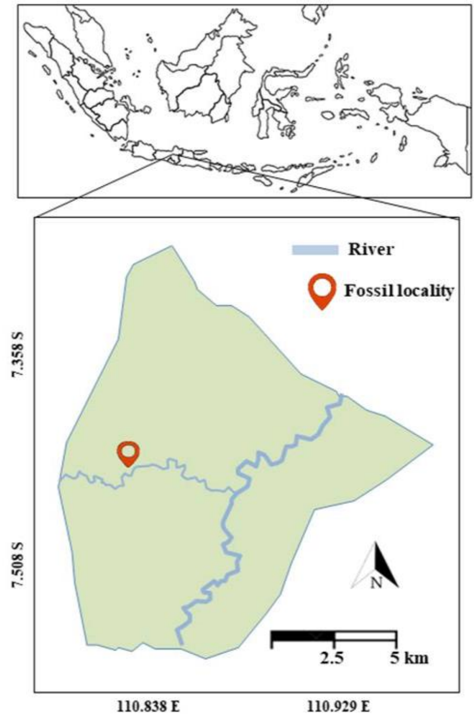

Figure 2. Locality of *Meganthropus palaeojavanicus* in Sangiran landscape of central Java.

Foraging ecology assessment

The assessment of *M. palaeojavanicus* foraging ecology was based on the comparison of home ranges to the close related hominid and extant large body size mammals. Australopithecoid and Neanderthal studies were used in this assessment (Henry et al. 2016). Reviews on the several literatures of the mammal body size and home range association have been performed to complete the assessments.

Results

Figure 3 present the forest cover and contour of Sangiran. Forest covers mostly dominated the west areas of Sangiran and the east areas have less covers. In west areas, the forest covered the landscapes from north to south. In east areas, the forest covers were more patchy and fragmented. The Sangiran was a hilly landscape. The west areas have more high grounds and hilly areas. While the east areas have more flat terrains. In west areas, the hills were crossed by the Cemoro river in the middle and this performed a valley landscape. The highest point in Sangiran was equal to 160 and located in the north west areas. The lowest point was at 91 m and mostly can be found in flat grounds at east areas and valley. The average slopes of the landscape was 7.5% and the maximum at the steepest point was 62.8%. The fossil of *M. palaeojavanicus* was found on the banks of the Cemoro river.

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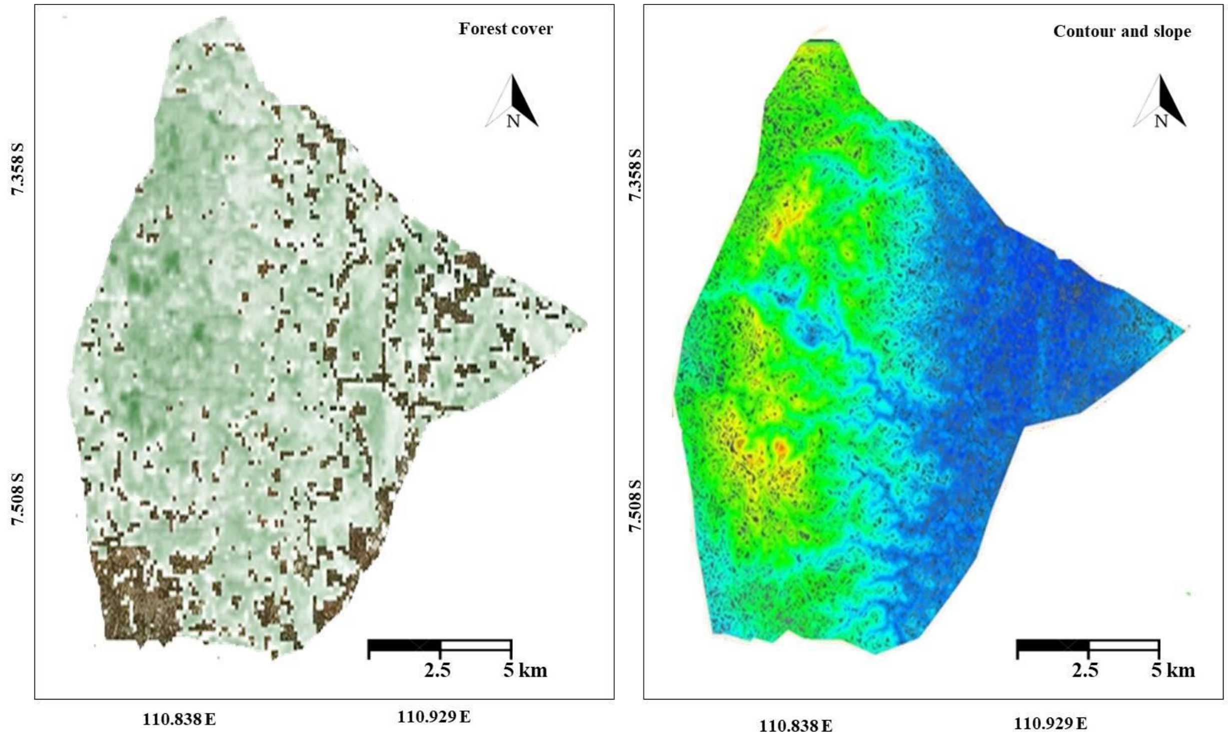

Figure 3. Forest cover (left) and contour of Sangiran landscape in central Java.

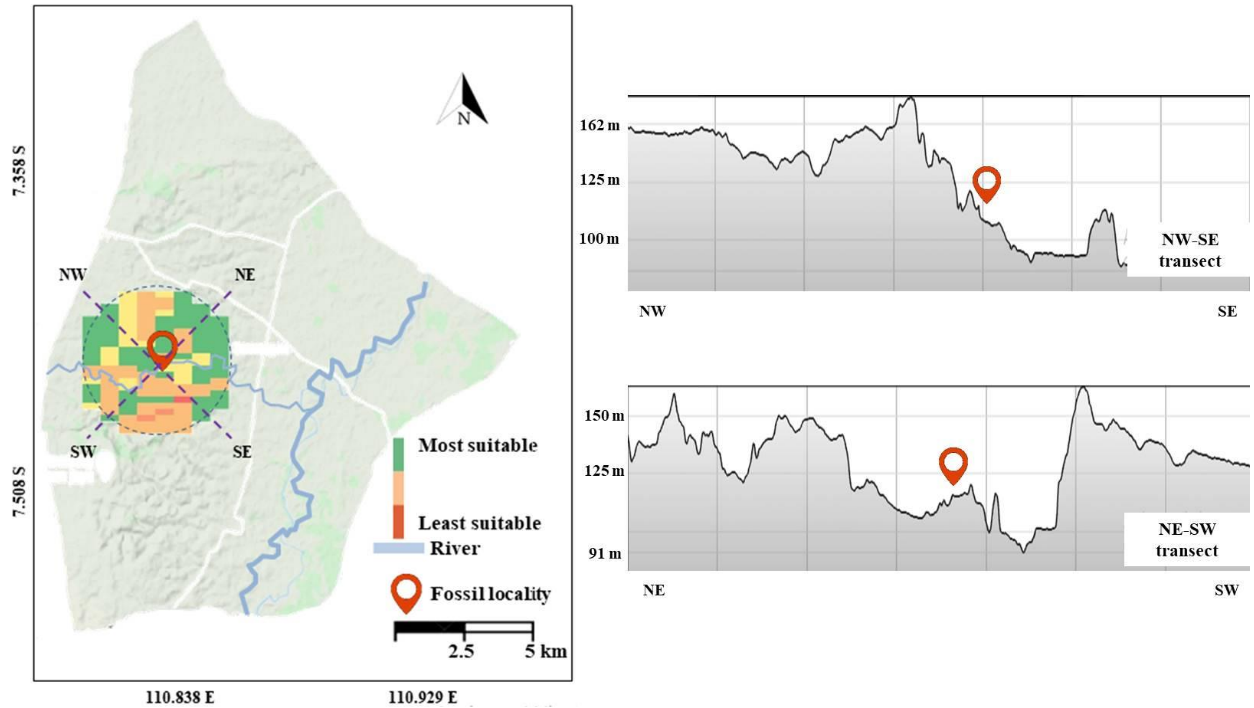

Figure 4. Model of suitable foraging areas within 5 km radius (left) and foraging area terrains in NW-SE and NE-SW 5 km directions (right) for *Meganthropus palaeojavanicus* in Sangiran landscape of central Java.

The suitable areas for foraging within 5 km radius were presented in Figure 4. The analysis shows that the most suitable areas were large in north east areas followed by north west and south east areas. South west areas have less suitable foraging areas. The terrains for foraging areas were also can be observed (Figure 4). The north east areas have more flat terrains than other areas. While north west (Figure 5) and south west areas were characterized by hilly landscapes with rugged terrain and steep slopes.

Figure 5 Hilly landscapes in north west areas of Sangiran in central Java.

Discussion

The foraging model developed in this study based on the interfaces of forest covers and terrains with the body sizes. Several extant and extinct species were using as comparison since the fossil remains of *M. palaeojavanicus* found in Sangiran was not complete. The fossil itself was found in the banks of Cemoro river at altitude of 110 m. The location was surrounded by hilly landscape and forest especially in northern areas.

Forest covers

Forest cover was an important determinant factor in determining the foraging ecology of species. This factor related to the food preferences and the biology of the studied species. Nonetheless, a study on dietary biology and foraging ecology of *M. palaeojavanicus* is still very limited. This constrained by limited numbers of fossil discoveries. Nonetheless, species that can be compared to *M. palaeojavanicus* was *austrolopithecus*. This corroborated by the study Orban-Segebarth and Procureur (1983) that state Asiatic *Meganthropus* originated from Sangiran has marked australopithecoid traits. This finding was based on biometric study comparing dental measurements of Sangiran *Meganthropus*.

In the foraging ecology model developed in this study, areas with dense forest cover were considered as more suitable foraging areas in comparison to barren lands. The areas dominated with the dense forest covers were hypothetically can provide more food for *M. palaeojavanicus.* Considering the morphological characters mainly on facial skeleton and molar characteristic lead to feeding mechanism of *M. palaeojavanicus*, this species has preference on certain food types as corroborated by study of Strait et al. (2009). Their study was based on australopithecoid traits that have similarity with *M. palaeojavanicus*. It was found that australopithecoid occlusal morphology is not well adapted to processing tough foods. Whereas its occlusal morphology was adapted more to eating stress-limited food items including seeds or nuts. During Pleistocene, seed and nut were produced by trees inside the forest (Jansen et al. 2012). Preferences of australopithecoid on closed woodland were also supported by Bobe et al. (2020). For large size mammals, forests were not required for foraging purposes only. Sanare et al. (2015) reported that forest covers were needed to provide protection, resting and sleeping areas.

River basin

Locality of *M. palaeojavanicus* in river bank indicated that water body plays important on the hominid presences. Besides *M. palaeojavanicus* there were several hominids found in the river bank. Another hominid was also found in small creek. Importance of water body to the hominid distribution has been discussed by Joordens et al. (2019). Related to the water body as habitats, riparian and basin were known contributing more on hominid abundances. High abundance of hominid in Afar Basin was related to the constant inputs from nearby Awash river draining from nearby highland. This condition explains the suitability of Sangiran landscape that receives water runoff from nearby hills.

Landscape terrain

Foraging ecology related to the body sizes and terrain and landscape have been discussed in many literatures. This area is very interesting and emphasizing more on how the large size mammal can cope the rugged terrain when forage. Nelleman et al. (2002) has used *Loxodonta africana*, an existing living largest mammal today, as a model to study the interfaces of body sizes and terrain. Variation in terrain did influence the foraging areas of *L. africana*.

Various terrain mainly rugged terrain contributed to the organism foraging activities related to the basal metabolism rate and energetic costs. Hominid living in rugged terrain has to minimize the energetic cost during foraging and this makes rugged terrain was not suitable. Landscape terrain in this study was modeled can limit the movement of *M. palaeojavanicus* considering its body size and energy cost. Using the most related extant species, Hanna et al (2008) confirmed that the consumed energy of primates whether climbing or walking a given distance was related to the body size. A negative correlation of mammals body size distribution with terrain ruggedness has been presented by Smith and Lyons (2011). A continent that has more rugged terrain will have less mammal species with large body sizes. While continent with less rugged terrain with low terrain ruggedness index in this case Africa (Nunn and Puga 2012) has more diversity of large size mammals. From this finding it can be inferred that large size hominid in this case *M. palaeojavanicus* may avoid rugged landscape.

Rugged terrain was hypothesized can benefit the hominid in the term of hunting activities. Henry et al. (2015) theorized that several hunting practices included thrusting or short-cast spears and close-up strategy or ambush were more effective undertaken in rugged, wooded landscapes rather than in open and flat terrains. Despites the benefit of rugged terrains, this situation was based on the Neanderthal species that has body size smaller than *M. palaeojavanicus*. Evidences on hunting in the forms of tools of *M. palaeojavanicus* were still lacking. Likewise, molar analysis on *M. palaeojavanicus* informs that this species has molar adapted more to consume seed, nut and grasses. Rugged terrain can also benefit organism to provide shelter from predators (Winder et al. 2012). Conversely, *M. palaeojavanicus* has a large body size and this will limit the risk of this species to be attacked by predator. In Sangiran landscape, the presence of Pleistocene predators was limited.

Despite aforementioned facts, there was still possibility of Sangiran rugged terrain explorations by *M. palaeojavanicus*. This due to the hand bone morphological development of australopithecoid that indicates a degree of manual dexterity and precision grip capability. Rey et al. (2011) stated that this capability will allow australopithecoid to perform rock climbing and negotiate significant terrain barriers include steep, rocky cliffs or blocky lava flows.

The preference of *M. palaeojavanicus* foraging areas toward flat terrain was also provided alternative food resources for this hominid species. In the Sangiran landscape, the flat terrains were dominated by shrub and this terrain was characterized by less forest covers. Vegetation adapted in these particular open and arid flat terrains was known as C_4/CAM vegetation. A hominid species was also known consuming C_4/CAM vegetation besides seed and nuts originated from closed woodlands. Based on Wynn et al. (2013), australopithecoid similar to *Meganthropus* was known consuming C_4/CAM including grasses, sedges, and succulents common in tropical savannas.

Conclusions

It was hypothesized that rugged terrain was preferred more by hominid. Nonetheless, this study offers an opposite theory by providing *M. palaeojavanicus* as a model. In here *M. palaeojavanicus* was modeled and preferred more the flat terrain rather than hypothesized rugged terrain. A predatory adoption strategy that makes hominid prefers more on rugged terrain was not applied since *M. palaeojavanicus* has large body size and this minimize this species risk to be hunted by predator. Furthermore, *M. palaeojavanicus* does not require rugged terrain for hunting purpose as theoritized in many literatures since *M. palaeojavanicus* consuming C_4/CAM vegetation that more available in flat terrains.

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