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## Human bipedalism and the importance of terrestriality: a reply to Thorpe et al.

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The paper by Thorpe *et al.* (above) follows on from our own paper (Winder *et al.* 2013); in setting out their view that bipedalism has arboreal origins, they present a critique of our hypothesis, which we address below.

We begin by observing that their views and ours are not in contradiction. We criticised ‘forest hypotheses’ of human evolution, not because we think they are wrong but because we think they are incomplete. In fact we agree with Thorpe *et al.* about the arboreal origin of bipedalism amongst certain groups of apes. What we are interested in, and what they do not address, is a different set of issues: how and why some apes, already perhaps pre-adapted to bipedalism in their anatomy, became committed to a terrestrial (non-arboreal) pattern of existence. We do not argue that upright posture cannot be explained by arboreal selective pressures, rather that such an explanation is not *ipso facto* sufficient to explain all hominin adaptations or produce *all* the features needed to survive on the ground.

We reject their view that our model suggests “a *single* newly identified driver; adaptation for ‘complex topographies’,” (Thorpe *et al.* above, p. 911; emphasis in the original). We wrote about *ecologically and structurally complex landscapes*, and used ‘complex’ or ‘rough’ topography as a proxy. Rough terrain is one of several characteristics all complex landscapes might be expected to share and which can be identified (at least to a degree) in the palaeoenvironmental record. We do not suggest that all terrestrial landscapes with rough terrain exert a uniform selective regime on their inhabitants—let alone a single selective pressure—not least because rough landscapes vary considerably in their vegetation cover. We also clearly stated that our model requires no assumptions about the anatomy or behaviour of the last common ancestor. It is thus not in any way incompatible with an arboreal, bipedal ancestry. On the contrary, it adds another layer to such a model, providing a ‘missing link’ between existing theories that work well for the earliest and latest periods of hominin evolution but not for the transition between them.

Thorpe *et al.* also criticise our hypothesis for not explaining why different characteristics of terrestrial bipedalism appeared piecemeal in the fossil record. However, it is a misconception to suppose that we proposed a single, simple selective pressure, which must necessarily act at a specific time in our evolutionary history. In fact, our model specifies a multi-stage trajectory, involving adaptation to complex landscapes as a first stage, and expansion beyond them through tactical use of terrain in a later stage. Central to our hypothesis is the importance of spatially and temporally heterogeneous landscapes, in which different hominin populations and species may occupy broadly similar—but not identical—niches.

Our hypothesis thus invokes a mosaic set of niches for early terrestrial hominins, albeit encompassed within a broader ‘complex landscape’ niche, such that different groups might be expected to diverge, adapt to the specific characteristics of differing landscapes, move

around, and periodically re-connect with other groups. This would fit well with the mosaic patterning and diversity of hominin anatomical adaptations we see in the fossil record.

Creatures adapted to complex landscapes might move on to specialise in a range of niches, requiring different sorts of locomotory and behavioural adaptations. Our argument is that complex landscapes provided a first step away from dependence on trees, followed by more widespread expansion through tactical use of topographic complexity, offering a *specific* trajectory for hominin evolution.

Finally, Thorpe et al. take us to task for failing to link particular environmental features with individual hominin species. We avoided this for two reasons. First, we did not wish to get bogged down in debates about taxonomy, species names and dates. Secondly, a mosaic evolutionary process is inherently complex and hard to reconstruct. Since we cannot identify all the characteristics of the particular complex landscapes that constrained the niches of specific groups, attempting to draw links between the anatomy of individual fossils and the nature of their particular environments is challenging and risky. The specific patterns we see are likely to be *emergent*—the result of chance, contingency and complex interactions—and therefore not predictable.

In conclusion, we emphasise that there is no necessary antagonism between the work of Thorpe *et al.* on the initial origins of bipedalism and our work on the subsequent history of the human lineage and the transition to terrestriality. Whether individual anatomical characters ultimately come to be seen as part of one phase or another is less important than the improvement in our overall understanding of human (and ape) evolution that comes from a consideration of landscape complexity.

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### **Reference**

WINDER, I.C., G.C.P. KING, M. DEVÈS & G.N. BAILEY. 2013. Complex topography and human evolution: the missing link. *Antiquity* 87: 333–49.