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Foraging strategy and tree structure as drivers of arboreality and suspensory behaviour in savannah-dwelling chimpanzees

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Introduction: The association between an open habitat (e.g., savannah-mosaics) and increased terrestriality is central to hypotheses of hominin evolution, especially the emergence and evolution of bipedalism, as well as ape evolution as far back as the early Miocene. However, the selective pressures that act on apes in an open habitat remain poorly understood. Observations of chimpanzees that live in savannah-mosaics, analogous to some reconstructed hominoid palaeohabitats, can provide valuable insight into the behavioural adaptations of a large-bodied, semi-arboreal ape to an open habitat, characterised by sparsely distributed food sources and a broken canopy. We previously showed that savannah-dwelling chimpanzees in the Issa Valley, western Tanzania, maintain a high level of arboreality, and particularly suspensory behaviour, largely associated with foraging. Here, we investigate how chimpanzee foraging strategy in a savannah-mosaic may drive a high frequency of arboreal behaviours despite reduced arboreal pathways. Specifically, we hypothesized that Issa chimpanzees would spend more time foraging (and moving) per tree to maximize utilization of food in a sparse landscape. This foraging strategy would be facilitated by foraging in trees with large crowns and abundant terminal-branch foods, which are characteristic of miombo woodlands. However, the link between foraging positional behaviour and tree structure remains understudied.

Methods: We collected data on arboreal foraging behaviour and corresponding tree structural characteristics over five months in the dry season, and used generalized linear mixed models to test for any effect of food type and tree structural characteristics on (1) duration of foraging bouts, (2) frequency of locomotion, and (3) use of suspensory behaviour.

Results: We found that food types and tree structures found in woodland vegetation are associated with more time spent in foraging trees, a higher rate of locomotion, and the use of suspension in particular.

Discussion: Our results suggest that arboreal, and especially suspensory, locomotion can be advantageous for foraging in a savannah-mosaic and not just closed forest habitats. These findings have implications for reconstructing hominoid positional behaviour from the fossil record and provide a model for how arboreality, and specifically suspensory behaviour, could have been an important part of the hominoid niche in savannah-mosaic habitats.

1 Introduction

Increased terrestriality, and correspondingly a reduced dependence on arboreal locomotor behaviours, has been considered an adaptive response to more open habitats in the evolution of some primate taxa, including cercopithecoids (e.g., McCrossin et al., 1998), capuchin monkeys (e.g., Falotico, 2011) and hominoids (i.e., living apes, including humans, and their extinct ancestors; e.g., Doran and Hunt, 1994; Sockol et al, 2007; Rodman and McHenry 1980). This association between terrestriality and open habitat has formed the basis of hypotheses seeking to explain the divergence of hominins (the human lineage), typically defined, at least in part, by morphological adaptations to habitual bipedalism, from panins (chimpanzees and bonobos) in the late Miocene (e.g., the savannah hypothesis, reviewed in Domínguez-Rodrigo, 2014). However, the porous hominin fossil record between 7–4 Ma (reviewed in Stamos and Alemseged, 2023) together with the virtual absence of an African ape fossil record (McBrearty and Jablonski, 2005; Suwa et al., 2007), means the evolutionary trajectory of hominins and panins from their last common ancestor, and the selective pressures that acted on them, remain poorly understood. Whilst palaeoenvironmental reconstructions support a shift from closed (e.g., tropical forest) to more open, heterogeneous environments (e.g., wooded, mosaic landscapes, hereafter "savannah-mosaic") early in hominin evolution (Levin et al., 2008; Cerling et al., 2011; Blumenthal et al., 2017; Negash et al., 2024; for review, see Su, 2024), there is mounting fossil evidence suggesting arboreality remained a vital part of the hominin adaptive niche (Alemseged, 2023; Cazenave and Kivell, 2023; but see Ward, 2002). Several extinct hominins have curved phalanges, relatively long upper limbs, and/or morphological features typically associated with arboreality, ranging from the late Miocene (e.g., *Orrorin tugenensis*, Senut et al., 2001; *Ardipithecus kadabba*, Haile-Selassie, 2001; *Sahelanthropus tchadensis*, Daver et al., 2022) to late Pleistocene (e.g., *Homo naledi*, Berger et al., 2015; *Homo floresiensis*, Larson et al., 2009). Furthermore, although there are limitations in paleodietary reconstructions, carbon isotope and dental microwear studies suggest certain hominins retained a diet with substantial arboreal food sources in environments with increasing C_4

vegetation (i.e. more open habitats) (Ungar and Sponheimer, 2011; Levin, 2015). In some cases, hominin diets are reconstructed as similar to those of extant chimpanzees (e.g., *Ardipithecus ramidus*, White et al., 2009; *Australopithecus anamensis*, Alemseged, 2015; *Australopithecus sediba*, Henry et al., 2012).

Among non-hominin apes, some large-bodied Miocene hominoids that show adaptations for arboreal locomotion have been placed in wooded, grassy habitats resembling savannah-mosaics as early as 21 million years (*Morotopithecus*, Peppe et al., 2023; *Kenyapithecus*, McCrossin et al., 1998). Together with hominin evidence, this brings into question the link between open habitat and the reduced importance of arboreal behaviour throughout hominoid evolution. Based on fossil evidence from Moroto, Uganda, MacLatchy et al. (2023) have further suggested that selective pressures associated with navigating open canopy to forage (rather than forest canopy with high connectivity, e.g., Ripley, 1979) may have driven the emergence of diverse orthograde arboreal locomotor behaviours in large-bodied apes.

In the absence of direct fossil evidence, extant chimpanzees (*Pan troglodytes*) that live in open and seasonal habitats analogous to palaeohabitat reconstructions for some hominoids can provide suitable models to test the "savannah effect" on ape behaviour (e.g., Moore, 1992, 1996; Pruetz and Bertolani, 2009; Lindshield et al., 2021, 2025; Drummond-Clarke et al., 2022, 2024; but see White et al., 2009). Chimpanzees (*P. t. schweinfurthii*) of the Issa Valley, western Tanzania, live in a savannah-mosaic habitat (Figure 1) that closely resembles the reconstructed palaeoenvironments of some late Miocene and early Pliocene hominoids (e.g., *Morotopithecus*, Peppe et al., 2023; *Graecopithecus*, Böhme et al., 2019; *O. tugenensis*, Pickford and Senut, 2001; *Ar. ramidus*, Levin et al., 2008, Negash et al., 2024; *Australopithecus afarensis*, Su and Haile-Selassie, 2022). Here, we investigated the role of foraging strategy and tree structure in an open habitat as drivers of arboreality and its associated positional behaviours, including suspension, in the Issa Valley chimpanzees.

Compared to forests, savannah-mosaics are generally considered to exert higher energetic stress on chimpanzees due to more sparsely distributed food sources (requiring more travel; Raichlen and
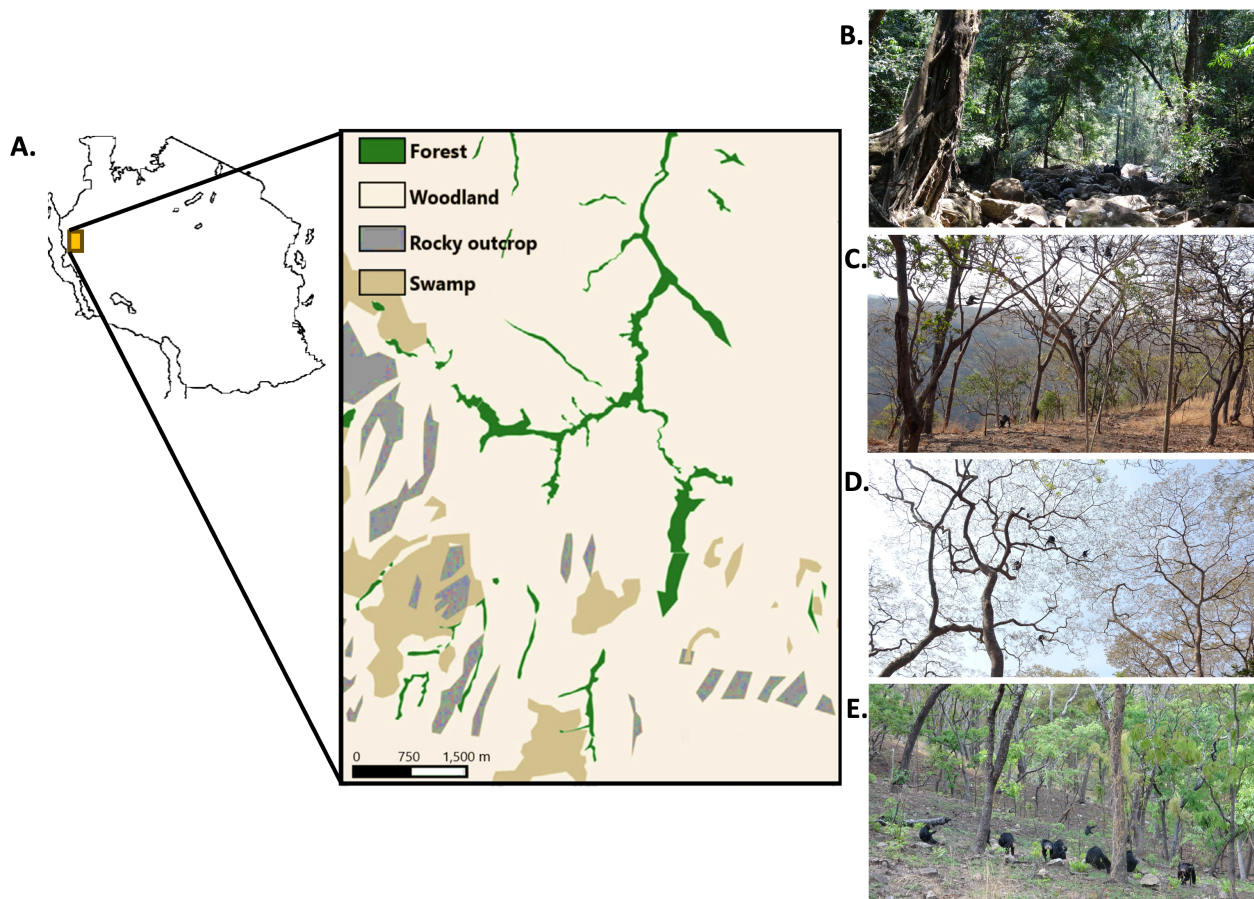
FIGURE 1
The Issa Valley study site. **(A)** Location in Tanzania and vegetation map. **(B)** An example of typical riparian forest vegetation at Issa during dry season (note dry river bed but evergreen vegetation). **(C−E)** Examples of typical miombo woodland vegetation during dry season at Issa. Woodland trees lose their leaves **(C, D)**, grass dries and is burnt by fires. The woodland undergoes regeneration with regrowth after fires **(E)**. Photo credits RCDC/ GMERC.

Pontzer, 2021) and high seasonality (McGrew et al., 1981; Kortlandt, 1983; Pruetz and Bertolani, 2009). Although findings of lower dietary diversity in savannah—compared to forest-dwelling communities (McGrew et al., 1988; Hunt and McGrew, 2002; Pruetz, 2006; Piel et al., 2017)—lend support to this concept (Vogel et al., 2017), savannah chimpanzees are not under higher nutritional stress compared to forest-dwelling populations (Wessling et al., 2018). Furthermore, bonobos living in forest-savannah mosaic habitats showed no difference in dietary diversity compared to their forest-dwelling counterparts (Pennec et al., 2020). This evidence could suggest that chimpanzees adjust their foraging strategy to counteract the high energetic demands of foraging on sparse food sources. Optimal foraging theory predicts that an animal will invest more energy (i.e., via time and movement) into foraging on patches of higher value, with time spent foraging in a patch used as a measure of patch value (Slocombe and Zuberbühler, 2006; Kalan et al., 2015; Villioth et al., 2022, Villioth et al., 2023). Patch value itself is suggested to be dependent on two factors. First, the energy return rate of the landscape, with lower food availability increasing the value of patches and thus time invested per patch (Charnov, 1976; Vogel et al., 2017).

This concept is supported by studies on spider monkeys (*Ateles belzebuth belzebuth*, Suarez, 2006) and Himalayan langurs (*Semnopithecus entellus*, Sayers et al., 2010). Second, the energy and nutrition available within the patch influences its value (Stephens and Krebs, 1986), which could be a function of patch size (i.e., larger size = higher value), food type and density within the patch (i.e., high density = high value), and, for social species, the amount of intraspecific competition (e.g., more conspecifics means less food per individual, as found for *Cebus imitator*, Vogel, 2005; cercopithecids, Janson and Goldsmith, 1995; *Pan troglodytes*, Lindshield, 2014, Villioth et al., 2022, Villioth et al., 2023). A foraging strategy of investing more time to high value patches, such as large trees with abundant foods, could therefore be an efficient way to maximise energy intake while foraging on sparsely distributed food sources (Chapman et al., 1995; Villioth et al., 2022).

In the first characterisation of savannah chimpanzee positional behaviour, we previously found that chimpanzees of the Issa Valley were just as arboreal, and in some cases more so, than chimpanzees at more forested sites (Drummond-Clarke et al., 2022; Drummond-Clarke et al., 2024). What is more, Issa chimpanzees used

comparably high frequencies of suspension and quadrupedal walking but less vertical climbing to navigate arboreal substrates, indicating horizontal movement on branches (rather than vertical movement on tree trunks as suggested by Senut et al., 2018) as an important component of their arboreal locomotor repertoire. These patterns raised questions as to why and how Issa chimpanzees maintain high levels of arboreality and, in particular, frequent locomotion on terminal branches, despite living in an open habitat with limited arboreal pathways. Notably, arboreal locomotion, and in particular locomotor (as opposed to postural) bipedalism, was used primarily for arboreal feeding at Issa (Drummond-Clarke et al., 2022). Suspension and assisted bipedalism are orthograde, horizontally-moving behaviours (Hunt, 1991; Hunt et al., 1996), that great apes can use in a continuum to navigate flexible terminal branches despite their large body size by distributing their weight across multiple supports (Thorpe et al., 2007b; Drummond-Clarke et al., 2022, Supplementary Video 1). Combined with a previous study showing the importance of forest architecture in shaping great ape locomotor behaviour (*Pongo*, Manduell et al., 2012), this supports a link between foraging positional behaviour and foraging tree structure (e.g., Crompton, 1984; Fleagle, 1979). We thus predicted that more time spent foraging on food items at the ends of branches specifically could drive the high frequency of terminal branch locomotor behaviours observed at Issa (Drummond-Clarke et al., 2022, 2024). However, whilst a basic link between substrate characteristics and ape locomotor behaviour is reasonably well established (e.g., suspension and assisted bipedalism on flexible substrates, climbing on vertical substrates; Hunt et al., 1996; Thorpe and Crompton, 2005, 2006; Manduell et al., 2012; Neufuss et al., 2017, 2018; Druelle et al., 2024; Drummond-Clarke et al., 2024), comparatively little is known about chimpanzee foraging strategy and substrate use in open habitats (reviewed in Lindshield et al., 2021), especially in relation to tree structure. Rather, existing studies on the relationship between tree structure and primate behaviour have focused only on tree size (Kalan et al., 2015; Villioth et al., 2023), nesting (e.g., Baldwin et al., 1981; Hernandez-Aguilar et al., 2013; Stewart and Pruetz, 2013; Samson and Hunt, 2014), or locomotor behaviour of other species (*Galago*, Crompton, 1984; *Pongo*, Manduell et al., 2012), severely limiting our understanding of how chimpanzee foraging behaviour and tree structure could be linked.

Here, we investigated chimpanzee arboreal foraging behaviour in relation to tree structure at Issa Valley to test the hypothesis that structural characteristics typical of woodland trees selects for the high levels of arboreality, and in particular arboreal locomotion and suspensory behaviour (Drummond-Clarke et al., 2022, 2024). Specifically, we predicted that foraging in larger trees with open and wide crowns, low connectivity and abundant terminal branch foods (characteristic of woodland feeding trees e.g., *Brachystegia* spp., Figures 1a, d) would not only drive longer foraging periods within tree crowns, but also more locomotion, and in particular suspensory behaviours, to navigate the terminal branch niche.

2 Materials and methods

2.1 The study site

The Issa Valley is a savannah-mosaic habitat located in western Tanzania (Figure 1). It is one of the driest areas known to be inhabited by chimpanzees, with a 6-month dry season spanning May–October, when grass fires burn >75% of the landscape (Piel and Stewart, unpublished data; van Leeuwen et al., 2020). The landscape is characterised by rugged topography (~1,050 to 1,750 m in elevation), dominated by miombo woodland vegetation (86%), while less than 7% of the vegetation is riparian forest (Figure 1a). Although there are also areas of seasonally inundated grasslands, chimpanzees were only observed foraging in the forest and woodland vegetation during the study period. The forest and woodland vegetation types differ significantly in aspects of vegetation structure that affect arboreal substrate availability; the miombo woodland vegetation is characterized by deciduous trees (predominantly *Brachystegia, Julbernardia* and *Isoberlinia* spp.) with discontinuous canopies and a grassy understory (Figures 1c–e), whereas riparian forest vegetation is characterized by evergreen and semi-deciduous trees with continuous canopies and open or liana-dense understories (Figure 1b; Russak, 2014; Drummond-Clarke et al., 2022). Compared to the forest, the woodland vegetation has lower species diversity and half the tree density (Piel & Stewart unpublished data) with significantly lower tree and crown height and canopy connectivity (van Leeuwen, 2019). We therefore consider the riparian forest as "closed" vegetation and the miombo woodland as "open". Importantly, whereas the forest vegetation undergoes little structural change throughout the year, the woodland is transformed during the dry season by trees shedding their leaves and grass fires that clear the ground vegetation from July to October. The fires, however, have a regenerative effect with regrowth of ground and tree vegetation occurring quickly after burning, even before the wet season begins (unpublished data). Fruit availability is highest in the late dry season when most fruit sources are in the woodland (Piel et al., 2017; Giuliano et al., 2022). In contrast, during the wet season, food availability is lower and most fruit sources are in the forest. Issa chimpanzees are known to forage in both riparian forest strips and miombo woodland, but concentrate their foraging efforts on woodland foods during the dry season (Piel et al., 2017; Giuliano et al., 2022), making them suitable subjects to investigate chimpanzee foraging behaviour in the dry and open extreme of their habitat range.

Importantly, stable isotope data and reconstructed floral and faunal assemblages indicate heterogeneous landscapes similar in floral (i.e., dominated by grassy woodland and riparian forest vegetation types) and faunal (e.g., cercopithecids, tragelaphines; White et al., 2009; Bobe and Reynolds, 2022; Negash et al., 2024) composition to Issa Valley (van Casteren et al., 2018; Piel et al., 2019). Moreover, the miombo woodland tree genus that now characterises Issa Valley, *Brachystegia*, with its large, open crowns and abundant terminal branch hard seed pods, may have been present in East Africa by the early Miocene (Bonnefille, 2010; Senut, 2021).

At the time of the current study, the habituated Issa community consisted of 29 individuals that were individually identifiable. We only

TABLE 1 The study sample by sex (and chimpanzee identity) and month.

Sample group	n Foraging bouts	% Woodland
Sex		
Female	174	68.97
Ba	23	
Co*	20	
Ju*	22	
Ka*	32	
Ki*	18	
Ko*	33	
Ma*	26	
Male	127	66.93
Bo	8	
Ki	14	
Mb	20	
Sam	34	
San	13	
Wa	29	
Wi	9	
Month		
June	38	57.89
July	38	60.53
August	73	72.60
September	86	73.26
October	66	66.67
Total	301	68.11

*Females with dependent offspring (defined as still suckling and being carried)
"% woodland" shows the percentage of observations that were made in the woodland as opposed to forest.

TABLE 2 Ethogram for variables measured during arboreal foraging bout observations.

Variable	Definition
Bout duration	Start-end time of the focal individual showing foraging behaviour to nearest second. If the focal changed activity for more than 10 seconds (Lindshield et al., 2017), or exited the tree, the bout was ended.
N locomotion	Number of occurrences of locomotion (displacement of centre of gravity) to move to a new "sub-patch" within the tree crown during a foraging bout.
N suspension	Number of occurrences of suspensory behaviour (centre of gravity is below the weight bearing structure. Shoulder and elbow joints fully extended, weight borne principally by forelimb(s)) during a foraging bout. Includes postural and locomotor suspensory behaviour.
Food type	Ripe fruit, unripe fruit, mature leaf, young leaf, bud, flower, bark*, seed (including pods), Pilostyles, insect*, sap*.
Food abundance	Absolute rating of abundance of food items in the tree crown on a scale of 1–5. 1 = very low, 2 = low, 3 = medium, 4 = high, 5 = very high.

*These food types were not included in analysis since there were limited observations (n < 3).

processing, and eating food), we recorded directly into an excel datasheet the start and end time [duration, ends when the focal clearly stops foraging and engages in another activity for more than 10 seconds following Lindshield et al. (2017), or exits the tree], number of bouts of locomotion (defined as the individual moving their centre of gravity, within the tree crown i.e., changing branches), number of bouts of suspensory behaviour, tree species, food type consumed (e.g., flower, leaf, fruit, seed), and food abundance within the crown (scale of 1–5, with 1 representing low abundance and 5 high abundance; Table 2). Suspensory behaviour was defined as postural and locomotor behaviours where the centre of mass is below the weight-bearing structure and the shoulder and elbow joints are fully extended, following Hunt et al. (1996) and Thorpe and Crompton (2006) (Supplementary Material 1; Supplementary Video 1). Trees were tagged and GPS-marked and were later returned to, to measure structural characteristics when the chimpanzees were not present (see below). Chimpanzees were observed foraging on arboreal food sources as well as lianas and some terrestrial foods. However, for this study we only analysed arboreal foraging bouts (excluding lianas) to investigate the potential relationship between arboreal positional behaviour and tree structural characteristics. Our previous studies of Issa chimpanzee positional behaviour revealed that suspension and assisted bipedalism were both used during arboreal foraging. However, bipedalism is a rare behaviour (0.8% of total observation time, Drummond-Clarke et al., 2022) and thus we were not able to collect sufficient data on bipedalism during the 5-month study period.

2.3 Foraging tree structure

Another observer, SCR, collected structural measurements of feeding trees. We recorded diameter at breast height (DBH) as a proxy for tree size, tree height (base of trunk to highest crown point), crown connectivity (scale of 0–100% contact around

included adults in this study, comprising a total of 14 individuals (7 males and 7 females, six of which had dependent young; Table 1). Non-adult individuals were not included as there was an insufficient number of individuals per non-adult age category for meaningful comparisons, and how chimpanzee foraging ecology may vary with age is poorly understood (Bray et al., 2018).

2.2 Foraging behaviour

One observer, RCDC, collected data on adult arboreal foraging behaviour during the dry season (5 months) using continuous focal sampling (Altmann, 1974). Focal subjects were observed at a minimum distance of 10m. Binoculars and a handheld camera (Sony AX53) were used to improve visibility when the focal was over 20m from the observer. When the focal individual began a foraging bout (marked by the start of an individual entering a tree and clearly collecting,

periphery of crown with neighbouring trees), crown shape [following categories outlined in Slater (2015) and van Leeuwen (2019)], crown base height (height above tree base to base of first principle branch), foliage base height (height above tree base of lowest tertiary branch), crown diameter (a mean of east–west and north–south diameters), number of boughs (primary branches attached to trunk), and number of secondary and tertiary branches (per diameter category; >20cm, 10–20cm, 3–10cm, <3cm; following (Hunt, 1992a; Doran, 1993a, 1993b; Drummond-Clarke et al., 2024). Further details of measurements and equipment used are outlined in Table 3 and Figure 2. We then calculated crown height (tree height – crown base height), foliage height (tree height

TABLE 3 Definitions and methods for measurement of tree structural characteristics.

Characteristic	Definition/details	Instrument used
DBH (cm)	Diameter of the tree trunk at breast height (1.5m from ground) (cm). See Figure 2.	DBH tape measure
Tree height (m)	To control for uneven terrain (researcher can be higher or lower than tree base), this was measured from the tree base point and the tree top height, using the 2-point height measurement function (available in rangefinders with inbuilt clinometer)*. See Figure 2.	Nikon Forestry Pro Rangefinder
Crown height (m)	The height of the lowest bough from the tree base was measured from eyelevel using the 2-point height measurement function*. See Figure 2. Lowest bough height was then subtracted from the tree height.	Nikon Forestry Pro Rangefinder
Foliage height (m)	The height of the lowest tertiary branch from the tree base was measured from eyelevel using the 2-point height measurement function*. See Figure 2. Lowest tertiary branch height was then subtracted from the overall tree height.	Nikon Forestry Pro Rangefinder
Crown diameter (m)	Measured along ground north–south and east–west. The mean of the two values was used in analyses. See Figure 2.	30m tape measure
Crown connectivity (%)	Measured as the amount of the tree crown touching neighbouring crowns, grouped between 0–25, 26–50, 51–75, 76–100.	Visual estimate
Number of boughs	Count of primary branches (connecting to tree trunk). See Figure 2.	Visual estimate
Number of branches	Count of secondary and tertiary branches within the crown per width category (cm): >20, 10–20, 3–10, <3** cm. See Figure 2.	Visual estimate
Tree shape	Classified as one of six crown shapes (see Figure 3), following van Leeuwen, 2019 and Slater, 2015.	Visual estimate

*Rangefinder height measurements were repeated 3 times per tree, or until sequential measurements were within 1m variation, to improve precision.
**Number of branches <3cm in diameter were estimated into categories following Manduell et al. (2012). Branches <3cm in diameter were excluded from subsequent calculations of crown density as they are too thin to be used individually as weight bearing structures by adult chimpanzees.

FIGURE 2
Schematic showing basic tree structural measurements. Heights were measured from tree base height using a rangefinder. Crown base height was measured as the height from the tree base to the first bough splitting from the tree trunk. Foliage base height was measured at the lowest splitting point of a tertiary branch from a secondary branch. DBH was measured with a DBH tape measure at chest height of SCR. Crown diameter was measured using a tapemeasure along the ground, and was measured n-s and e-w then averaged. Drawn from an image of a *Brachystegia microphylla* at Issa Valley, characteristic of an upside-down cone shaped woodland tree. Credit RCDC.

– foliage base height), relative foliage and crown width ratios (by dividing foliage or crown height by average crown diameter, whereby a larger value = wider crown), and crown density (the sum of secondary and tertiary branches >3cm divided by DBH).

2.4 Data analyses

We performed all analyses in R v 4.4.0 (R Core Team, 2023) and set the significance level alpha at 0.05. We produced summary statistics for variables measured using summary SE function (emmeans package; Lenth, 2024). We ran Mann-Whitey-U and Welches t-tests to test significance of the difference between means for feeding tree structural characteristics between vegetation types, since the data were not always homogenous in variance or normally distributed. Both tests gave similar p-values, so only Welches t-test results are discussed due to their greater power and conservatism against type I errors based on our sample sizes (Zimmerman, 1987; Ergin and Koskan, 2023).

Before constructing generalized mixed linear models (see below), we checked for strong correlations between tree structural variables using function ggairs (package GGally; Schloerke et al., 2024), and used only non-correlated variables in models to avoid problems of collinearity between model covariates. For example, we found DBH to be significantly positively correlated with tree height, crown height, crown diameter, and each branch number category, so we chose to keep only DBH as an explanatory variable in model fitting (as a proxy for overall tree size), and used relative measures of crown diameter:height and crown density to model the effect of crown characteristics, rather than size. We also grouped food types into larger categories based on general ecological similarities (e.g., Conklin-Brittain et al., 1998) to investigate questions of general food characteristics (e.g., nutritional content, hardness) on foraging behaviour. Specifically, unripe fruit was kept separate to ripe fruit due to its higher (hard to process) fibre content (Conklin-Brittain et al., 1998). Flowers and buds were grouped with leaves as "soft non-fruits" due to the small sample size of flower foraging and similarities in processing and distribution in tree crowns, as well as macronutritional values (e.g., high crude protein content; Conklin-Brittain et al., 1998, Conklin-Brittain et al, 2006). Seeds were kept separate from other non-fruits due to their unique mechanical properties (mostly encased in woody pods/exocarps with high hardness, toughness and stiffness; van Casteren et al., 2018), which has been shown to affect food choice in apes (*Pongo*, Vogel et al., 2009), and likely nutritional/energetic values (e.g., higher lipid content; Conklin-Brittain et al., 1998, 2006). We also separated *Pilostyles aethiopica* (Bellot and Renner, 2014; hereafter *Pilostyles*), a holoparasitic epiphyte that grows inside the terminal branches of host woodland tree species, into their own category. *Pilostyles* are distinct relative to other chimpanzee foods given their unusual nature; they are very small and densely spaced "buds" that emerge from the host's bark, making it difficult to discern if they are flower or fruit when being eaten, and they were consumed at a high

frequency during the study period. The final food categories used were: ripe fruit, unripe fruit, soft non-fruit (mature and young leaves, buds and flowers), seeds, and *Pilostyles*.

We used generalized linear mixed models (GLMM; glmmTMB package; Brooks et al., 2017) to evaluate the effects of tree structure and food type, as well as other covariates (sex, vegetation type, month) on the rate of locomotion (modelled as the rate of locomotion per minute; negative binomial distribution), occurrence of suspensory behaviour (absent = 0, present = 1; binomial distribution), and duration of foraging bouts (gamma distribution). All three models included focal individual, date, and tree species as random intercepts to control for temporal and individual variation. Crown density was quadratic in nature (rather than non-linear) and thus squared to improve model fit. We included the log-transformed duration of bout as an offset to control for varying lengths of observation period (i.e., foraging bout duration) and allow modelling of predictor effects on rate of locomotion, rather than on raw count. Suspension is a relatively rare behaviour and therefore to improve modelling power, we used a presence/absence binomial approach, marking all bouts with observed suspensory behaviour as 1, and bouts with no suspensory behaviour as 0. For each response variable, we compared subsets of explanatory variables and their interactions to test our hypotheses using the dredge function and model averaging (MuMIn package; Bartoń, 2023). Models were selected using ΔAIC < 2. Both full and conditional model-averaged coefficients are presented in the supplementary material. While full averaging provides a conservative estimate (reducing Type-I errors), conditional averaging avoids excessive shrinkage allowing discussion of important effects in the best supported model. Since in each case only two models were averaged, we present only the conditional averaging below, focusing on variables present in at least one top model. As a summary of goodness-of-fit, we checked that the AIC of the full model (including both fixed and random effects) was smaller than that of the null model (containing only fixed effects; Akaike et al, 1973), and report the explained variance of the data by the model (coefficient of determination, R^2) using the r.squarredGLMM function (MuMIn package; Bartoń, 2023) following Nakagawa and Schielzeth (2013) (Supplementary Materials 2–4). We verified model fit by plotting residuals using DHARMa package (Hartig, 2022; Supplementary Materials 2–4). Since assumptions of homoscedasticity and normality of residuals were met for all final models, we conducted *post-hoc* Tukey tests to examine pairwise comparisons within categorical variables, adjusting for multiple comparisons (Supplementary Materials 2–4).

3 Results

The final sample of arboreal foraging bouts is outlined in Table 1. We recorded a total of 301 arboreal foraging bouts by adult females and males in 203 trees for which the structural characteristics were measured. Below we give an overview of Issa

chimpanzee arboreal foraging behaviour during the dry season, followed by the final model outputs for factors affecting arboreal foraging behaviour (duration, rate of locomotion, and use of suspensory behaviour).

3.1 Arboreal foraging variables

During the observation period, the mean number of locomotor bouts per foraging bout was 2.13 ± 0.16, the mean number of suspensory bouts was 1 ± 0.09, and the mean duration of foraging bouts was 19.83 ± 1.08 mins.

3.1.1 Dry season arboreal dietary patterns

During the study period, Issa chimpanzees foraged on a minimum of 28 different tree species (27 known species, 1 unknown category grouping multiple species), of which 16 were forest species, 23 were woodland species, and 11 species were

recorded in both vegetation types. Fruits were the most frequently eaten arboreal food type (48%; comprising 42% ripe and 6% unripe), followed by soft non-fruits (32%; comprising leaf 22%, bud 6%, flowers 3%), *Pilostyles* (12%), and seeds (9%), respectively. In keeping with previous studies that also included non-arboreal foods (Giuliano et al., 2022; Piel et al., 2017), Issa chimpanzees fed in trees mostly in woodland vegetation (68% of total feeding time) during the dry season. Their arboreal diet was also more varied in the woodland, with forest-tree foraging consisting almost solely of fruits, whereas woodland-tree foraging was spread across fruit, soft non-fruits, *Pilostyles*, and seeds (Figure 3A). Notably, seeds (Figure 3C) and *Pilostyles* (Figure 3D) were exclusively woodland foods. All foods were located in the terminal branches of the feeding trees and the majority of observed arboreal foraging bouts were in tree crowns with high to very high abundance food items. However, by food category only *Pilostyles* were fed on almost exclusively when very highly abundant within the tree crown (>80% of time), with only half of observed arboreal foraging bouts on fruits and soft non-
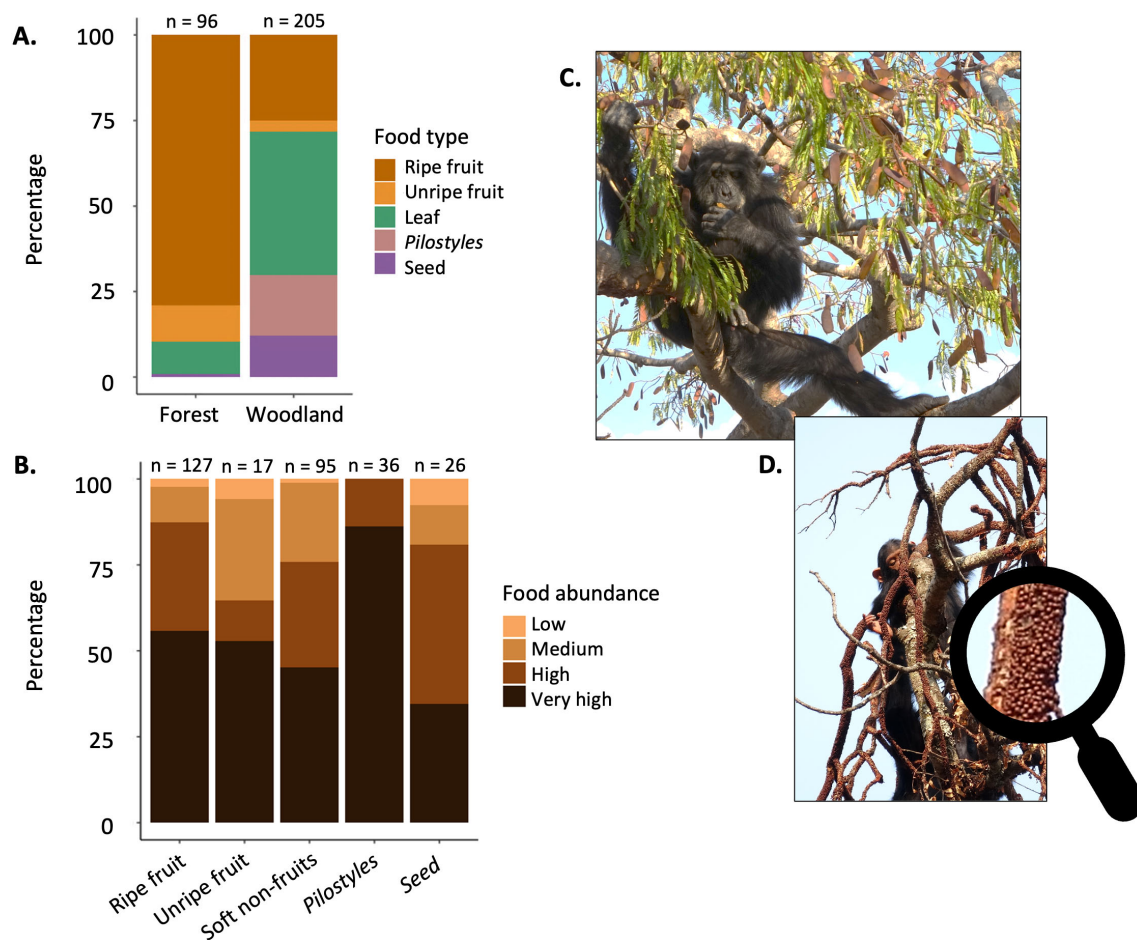

FIGURE 3
Patterns of arboreal foods consumed over the study period at Issa Valley. **(A)** Percentage of arboreal foods consumed per vegetation type. Arboreal forest feeding consisted mainly of fruit, whereas arboreal woodland feeding was more distributed across food types, with non-fruits making up the majority of woodland arboreal foods. **(B)** Percentage of trees per food type foraged in during the study period with low abundance to very high abundance food items, per food category. Note *Pilostyles* were the only food items to be foraged in trees with highly to very highly abundant food items. No observations were made of chimpanzees foraging in trees with a food abundance of level 1 during the study period. **(C)** Photo example of tough seed pods characteristic of woodland (*Brachystegia microphylla*), and **(D)** photo example of *Pilostyles aethiopica*, growing on a woodland tree. N feeding bouts = 301. Photo credits RCDC/GMERC.

fruits, and 30% of observed arboreal foraging bouts on seeds in trees with very highly abundant food items (Figure 3B). In further contrast, over one third of observations of arboreal foraging on unripe fruit were in crowns with low to medium food abundance, more than any other food type (Figure 3B).

3.1.2 Feeding tree structural characteristics

The mean DBH of foraging trees was 45.70 ± 1.59 cm, but foraging trees had a significantly larger DBH in the forest (60.97 ± 4.02cm) than in the woodland (38.56 ± 1.09cm, welches t = 5.38, p < 0.0001). The mean crown diameter of feeding trees was 10.84 ± 0.25m and did not vary significantly between vegetation types (t = 0.03 p = 0.975). However, crown height was significantly higher in the forest (7.94 ± 0.45m) than in the woodland (6.47 ± 0.21m; t = 2.94, p = 0.004), as was overall tree height (forest = 17.32 ± 0.64m, woodland = 12.84 ± 0.25 m, t = 6.47, p < 0.0001). Whereas the crown width:height ratio was not significantly different between vegetation types, the foliage width:height ratio was significantly larger in woodland (2.73) than in the forest (2.11; t = −2.90, p = 0.004). Woodland trees also had a significantly higher density of branches between 3–20 cm in diameter than forest trees (t = −3.51, p = 0.0006). Upside-down cone was the most common tree shape in which chimpanzees foraged, followed by spheroid trees in both vegetation types. Chimpanzees only foraged in umbrella-shaped trees in the woodland (Figure 4).

3.2 Model outputs

Results from the GLMM show that the duration of foraging bouts was strongly positively correlated to the use of locomotor behaviours, as well as the use of suspensory behaviour specifically (Table 4). Sex, vegetation type, and month were not significant in any model. The final models for bout duration, rate of locomotion, and occurrence of suspensory behaviour whilst foraging are presented below and in Table 4.

3.2.1 Foraging bout duration

The results of the GLMM investigating potential influences on foraging bout duration showed that tree DBH, food abundance, and food type have a significant effect on foraging duration (Table 4). As expected, DBH and food abundance were positively associated with longer foraging bouts. Chimpanzees spent a significantly longer amount of time foraging in trees with very highly abundant food (level 5), showing little difference between lower food abundance levels [although note low abundance (level 2) had a very large variation due to the small number of observations, and there were no observations of chimpanzees foraging in a tree with a very low food abundance (level 1; Figure 3B; Supplementary Material 2)]. Foraging on seeds and unripe fruit was associated with longer foraging bouts (average >25 min.), followed by Pilostyles (24 min.), ripe-fruit (20 min.), then soft non-
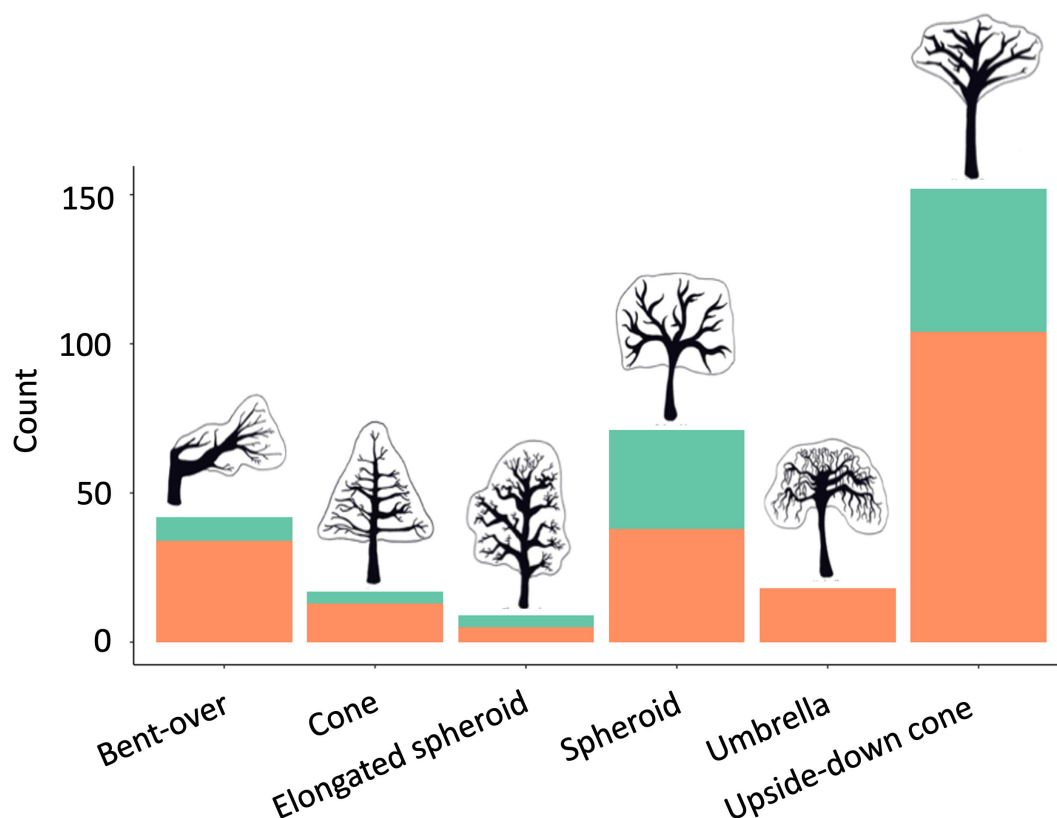

FIGURE 4
Tree shape used during foraging in each vegetation type (woodland = orange, forest = green). Chimpanzees only foraged in umbrella-shaped trees in the woodland. Tree shape schematics taken from Slater (2015).

TABLE 4 GLMM results for food and tree structural variable's influence on Issa chimpanzee arboreal foraging behaviour.

Term	Chisq	Df	Pr(>Chisq)
Response = foraging bout duration, family = gamma. AIC 2361 (null = 2399)			
Intercept	14.48	1	< 0.001 ***
DBH	6.98	1	0.008**
Food abundance	24.28	3	< 0.001 ***
Food type	19.28	4	< 0.001 ***
Crown density	0.03	1	0.867
Food type * crown density	13.37	4	< 0.01**
Response = rate of locomotion, family = negative binomial. AIC 1021 (null = 1061)			
Intercept	332.53	1	< 0.001 ***
Food type	12.11	4	0.02*
Crown density	4.29	1	0.04*
Response = occurrence of suspension, family = binomial. AIC = 386 (null = 395)			
Intercept	7.59	1	0.006**
Duration	21.42	1	< 0.001***
Foliage width:height	5.58	1	0.018*
Tree shape	10.71	5	0.057

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

fruits (12 min.) (Figure 5A). *Post-hoc* Tukey tests, however, showed only foraging bouts on seeds were significantly longer than foraging bouts on soft non-fruits (estimate = −0.77, p = 0.001), although the difference in foraging time between seeds and ripe fruit approached significance (estimate = −2.68, p = 0.058). In the best fitting model, food type had a significant interaction with crown density; lower crown density was associated with longer foraging bouts for unripe fruit and seeds, although crown density did not affect duration when foraging on ripe fruit, soft non-fruits, or *Pilostyles* (Figure 5B).

3.2.2 Frequency of locomotion

The best-fitting model revealed food type and crown density as significant factors influencing the frequency of locomotion. Specifically, foraging on unripe fruit had the highest average frequency of locomotion (Figure 5C), although *post-hoc* tests show it was only significantly more than foraging on seeds (estimate = 0.99, p = 0.008) and soft non-fruits (estimate = 0.72, p = 0.032; Supplementary Material 3).

3.2.3 Use of postural and locomotor suspension

Apart from duration of foraging bout, tree structural characteristics (rather than food type) had the most significant effect on the use of suspension during foraging; foliage width:height ratio was significant, and tree shape approached significance. Against expectations, trees with relatively narrower crowns/foliage

were more associated with the use of suspension during foraging. Trees with umbrella- or upside-down cone-shaped crowns had a significantly higher likelihood of suspensory behaviour being used during foraging (Figure 6), although *post-hoc* Tukey tests show only umbrella-shaped trees as significant compared to bent-over trees (estimate = −2.20, p = 0.046; Supplementary Material 4).
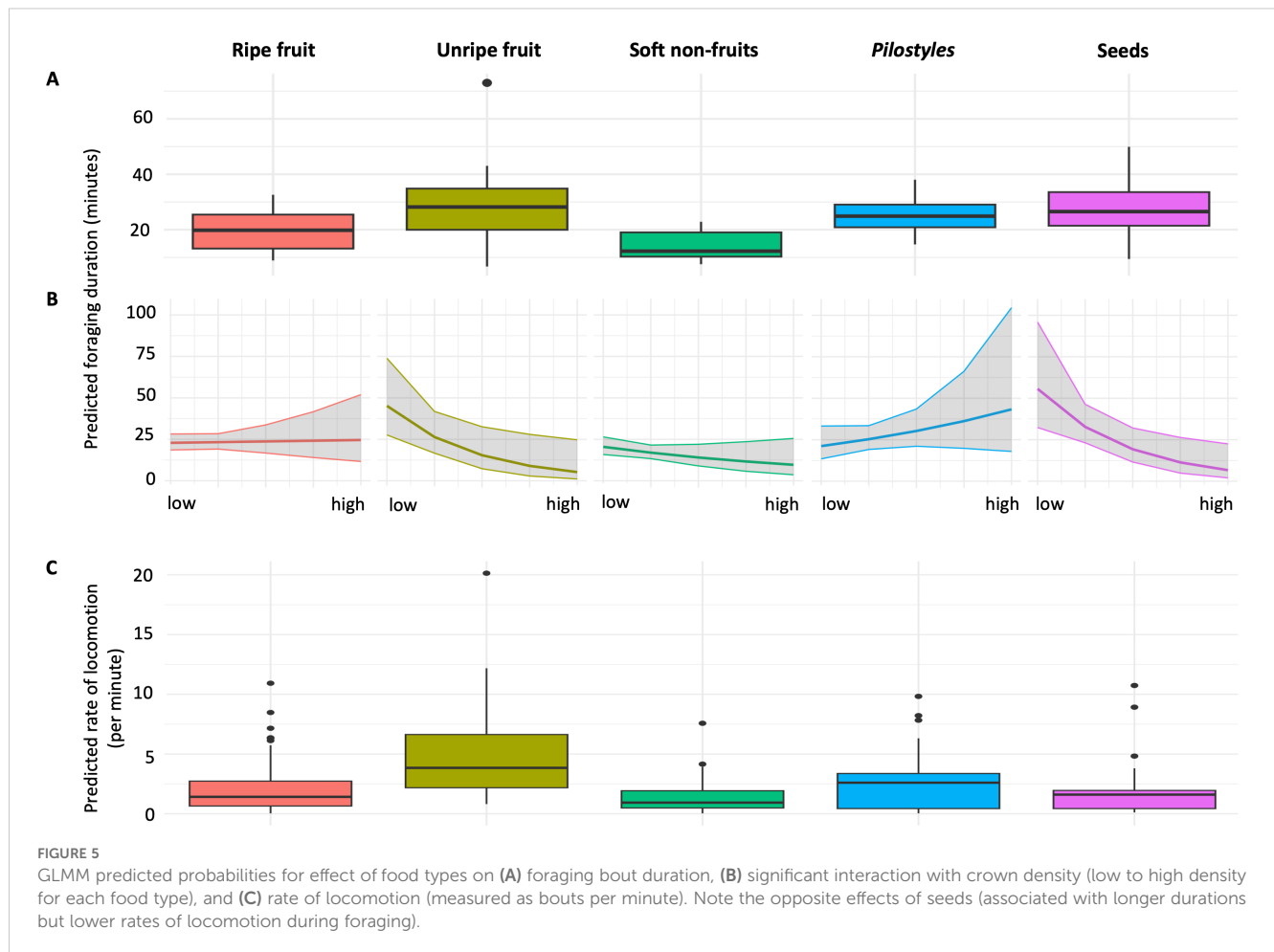
4 Discussion

In this study, we investigated the role of chimpanzee foraging strategy on substrate use and positional behaviour in an open habitat. We tested the hypothesis that foraging for longer in large, open tree crowns with abundant terminal branch foods (characteristic of woodland feeding trees such as *Brachystegia* spp.; Figures 1c, d) would drive the high frequency of arboreal locomotion and specifically suspensory behaviour previously described for Issa Valley chimpanzees (Drummond-Clarke et al., 2022; Drummond-Clarke et al., 2024). Our study is the first to test the link between chimpanzee arboreal foraging behaviour and foraging tree structure, allowing us to shed light on the selective pressures shaping chimpanzee positional behaviour in a savannah-mosaic habitat.

4.1 Foraging strategy and tree characteristics

We found that foraging on terminal branch foods in trees with large, open crowns and high food abundance (and specifically on seeds and unripe fruit) was associated with longer foraging bouts, and subsequently more arboreal locomotor behaviours (including suspension). Following predictions of optimal foraging theory that an animal will invest more energy into food patches of higher value (e.g., Chapman et al., 1995; Villioth et al., 2022), it is not surprising that longer foraging bouts were associated with larger trees with more abundant food at Issa, as we predicted. Foraging in higher value food patches likely provides a higher energy rate of return than foraging in small or food-depleted trees (Chapman et al., 1995; Villioth et al., 2022). Our results also showed that food type was an important factor determining time spent foraging in a tree, with foraging on unripe fruits and seeds associated with the longest foraging bouts. We suggest this may be due to longer processing times needed per food item, which increases the time to deplete the patch and thus foraging duration. In support of this hypothesis, the majority of seed species fed on during our study period were encased in tough seed pods or exocarps (e.g., *Brachystegia* and *Julbernardia* spp.; van Casteren et al., 2018) that require time to open and access the seeds inside. Compared to ripe fruits, unripe fruit is also generally higher fibre, which is harder to process (Conklin-Brittain et al., 1998) and thus may also increase processing time.

Alternatively, the optimal diet framework predicts that animals favour foods with maximum energy returns (or higher profitability), such as higher caloric yield (Emlen, 1966; Stephens

FIGURE 5
GLMM predicted probabilities for effect of food types on **(A)** foraging bout duration, **(B)** significant interaction with crown density (low to high density for each food type), and **(C)** rate of locomotion (measured as bouts per minute). Note the opposite effects of seeds (associated with longer durations but lower rates of locomotion during foraging).

and Krebs, 1986; Vogel et al., 2017). Whilst further analyses are required for nutritional content of foods at Issa, seed pods are relatively large food items that have multiple seeds inside with high protein content (Conklin-Brittain et al., 1998; Conklin-Brittain et al., 2006). Therefore, more time can be invested into processing seed pods as they may offer a higher caloric return. Additionally, analyses of chimpanzee foods from other communities suggest leaves and flowers are of lower profitability than fruits (Lindshield, 2014), which may explain their association with shorter foraging bout durations. Further study of food availability and energy return rates for different foods, including non-arboreal foods, within the Issa landscape and in comparison, to other chimpanzee sites will be vital to further test whether savannah-mosaic environments select for a foraging strategy of longer foraging durations per tree due to overall low food density/low energetic return across the landscape (e.g., Charnov, 1976; Vogel et al., 2017). Such data will also be insightful to test how factors like regrowth after burning may influence foraging strategy. For example, we found that soft non-fruits (i.e., leaves and flowers) were associated with the lowest foraging duration and rate of locomotion per tree of all food types, and were very abundant across the woodland during the post-burning leaf-flush.

4.2 Foraging strategy and arboreal locomotion

Whilst more time spent foraging in a tree was associated with locomotor bouts, a higher rate of locomotion (i.e., locomotor bouts per minute) was associated with denser crowns and certain food types. Specifically, unripe fruit was associated with longer foraging durations and higher rates of locomotion while seeds were associated longer duration but low rates of locomotion. This difference may be related to differences between overall patch (or tree) depletion versus depletion of the particular area of the tree the chimpanzee can access without moving (i.e., the food within arms-reach from a branch, hereafter referred to as "sub-patch"). In other words, food items that require more processing time, such as seeds (van Casteren et al., 2018), will not only take longer to deplete the entire patch but also to deplete the accessible sub-patch, resulting in less movement within the tree per time unit (e.g., optimal foraging theory on the scale of the "patch" rather than the landscape; Charnov, 1976; Stephens and Krebs, 1986).

A lower rate of locomotion associated with some food types may also relate to foraging technique. In particular, chimpanzees have been observed to sit/stand on secondary branches and reach,
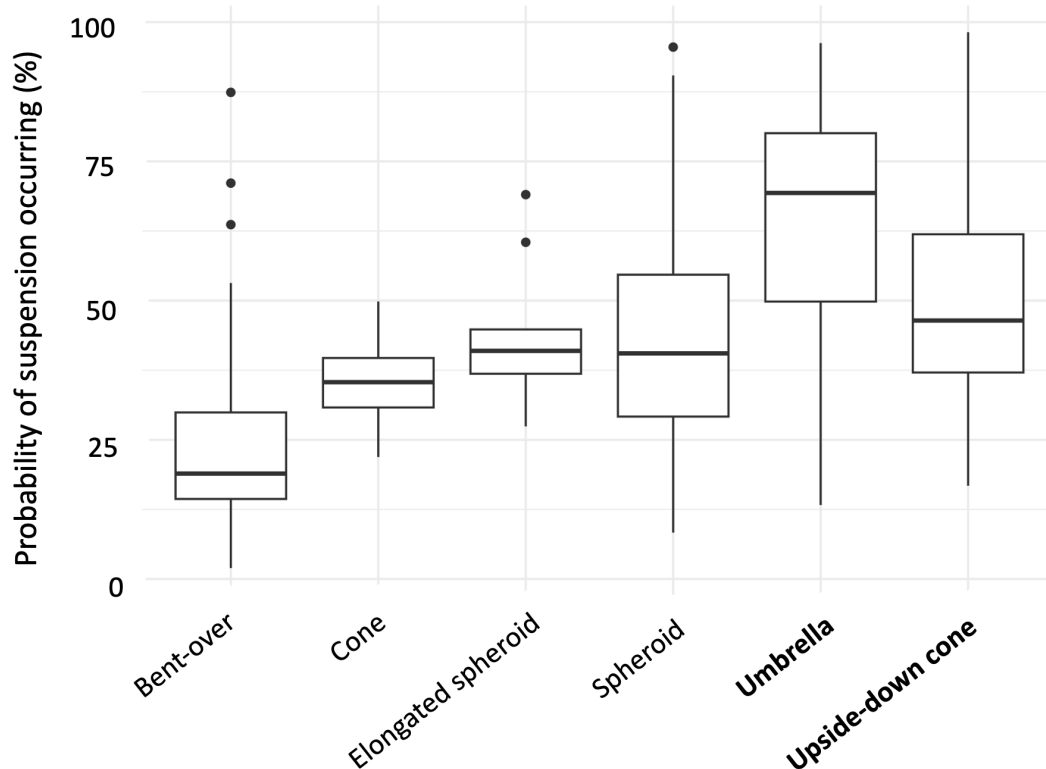
FIGURE 6
Predicted probabilities of the occurrence of suspensory behaviour (posture and locomotion) for tree shape. Crown shapes in bold are those with significantly higher probabilities of suspension occurring (reference level = bent-over crowns).

grab, and fold in tertiary branches to bring nearby food sources to them, rather than moving (e.g., Fruth and Hohmann, 1996; Wrangham, 1975; RCDC, personal observation). This effectively enlarges the sub-patch foraging area (and energetic value), which could explain the low rates of locomotion associated with foraging on leaves, *Pilostyles*, and seeds observed at Issa. Further research is required to investigate whether particular food (i.e., distribution or mechanical properties; van Casteren et al., 2018; Neufuss et al., 2019) or tree structural characteristics (i.e., crown density, branch compliance) select for such a technique (e.g., Stewart, 2011; van Casteren et al., 2012, van Casteren et al., 2013; Hernandez-Aguilar et al., 2013; Samson and Hunt, 2014; Lacroux et al., 2023), and if these could be associated with qualities characteristic of savannah-mosaic vegetation such as open crowns and tough foods.

Further research into the link between food characteristics and processing technique would also be informative for investigating the role of crown branch density on arboreal foraging behaviour. Whereas overall, we found that foraging in trees with higher branch density was associated with a higher rate of locomotion (supporting a link to substrate availability e.g., Manduell et al., 2012), the link between crown density and foraging bout duration was not so straightforward. Specifically, foraging in more open tree crowns was associated with longer foraging bouts only when foraging on unripe fruit and seeds, but not other food types. This suggests that processing time/technique plays a role, but further

work is also required on differences on food distribution within the crown (i.e., clumped or dispersed) of different food types.

We acknowledge that we did not account for factors that influence foraging behaviour, such as group size and composition (Lindshield et al., 2017; Villioth et al., 2022; Villioth et al., 2023), and food availability and distribution (e.g., Charnov, 1976), which are likely themselves interrelated (Fimbel et al., 2001; Giuliano et al., 2022). For example, Sonso (Budongo, Uganda) chimpanzees (*P. t. schweinfurthii*) feed in larger patches for longer durations, and travel further between patches when in larger groups (Villioth et al., 2022). Further, low-ranking chimpanzees are likely to alter their use of the tree crown (M-group, Mahale, Tanzania, Hunt, 1992b, Hunt, 1994a) and feeding rate (Fongoli, Senegal, Lindshield et al., 2017) depending on group size and composition, which would influence locomotor behaviour within a patch. Combined with findings that savannah chimpanzees are more cohesive than forest communities (Mount Assirik, Tutin et al., 1983; Fongoli, Pruetz and Bertolani, 2009; Issa, Giuliano et al., 2022), habitat could have an important effect on chimpanzee foraging tree choice and thus positional behaviour. Future studies should focus on quantifying foraging group composition in conjunction with distance between patches and food availability across the Issa Valley—importantly including terrestrial foraging—to test the role of habitat energy return rates and conspecific competition on foraging strategy in a savannah-mosaic. Further investigation of these factors at Issa could explain

why, for example, unripe fruit was the only food type that was associated with both a long duration of feeding and a high rate of locomotion.

4.3 Foraging tree structure and suspensory behaviour

Multiple studies have previously linked the use of suspensory behaviour to navigating thin and flexible terminal branches (e.g., Hunt et al., 1996; Thorpe et al., 2007a, 2007b). We therefore predicted that the high rate of suspensory behaviour previously observed at Issa (Drummond-Clarke et al., 2022, 2024) was driven by foraging in large trees with wide, open crowns and abundant terminal branch foods; specifically, by driving the chimpanzee to move around the tree crown, on thin, non-vertical, and compliant branches (or terminal branches). This would require them to transfer their weight below the branch, to access foods efficiently before exiting the tree. Supporting our prediction, the use of suspensory behaviour was associated with tree structure. However, contrary to our expectations, trees with larger height-to-width ratios (i.e., relatively tall, rather than short wide crowns) were associated with a higher likelihood of suspensory locomotion. Since there was no difference between vegetation types in mean crown diameter (average 10 m), we suggest that there was insufficient variation in crown diameter between feeding trees to have a significant effect on behaviour. Rather, tree height showed more variation and had a stronger correlation to DBH (i.e., our proxy for tree size) than crown diameter, meaning trees with taller crowns may have larger crowns overall, providing more available (terminal branch) substrates on which to suspend.

Suspensory behaviour was associated with upside-down cone- and umbrella-shaped trees. Upside-down cone-shaped trees are the predominant tree shape across the Issa Valley and characteristic of the woodland. Moreover, umbrella-shaped trees were only foraged in the woodland during the study period, despite also existing in the forest, highlighting the fact that features of open habitats can drive suspensory behaviour despite fewer arboreal pathways. Our finding that the use of suspensory behaviour was related to tree shape suggests that structural aspects of the tree not captured in our other tree measurements (e.g. crown diameter, crown width) likely affect the use of specific positional behaviours. For example, branch angle, length, or compliance may be more important than the other structural characteristics that we measured (e.g., van Casteren et al., 2013; Senut et al., 2018; Druelle et al., 2024; Janisch et al., 2024). Upside-down cone- and umbrella-shaped trees are characterised by long, horizontal/diagonal branches that may be more flexible than shorter branches (van Casteren et al., 2013). Navigating the terminal branches of such trees could therefore select for suspensory (and bipedal) behaviour to access foods at the end of flexible branches (e.g., Thorpe et al., 2007a, 2007b). More studies of branch/substrate characteristics, such as compliance, in wild and captive settings will be critical to improve our understanding of the link between navigating the terminal branch

niche and the use of positional behaviours such as suspension and bipedalism.

4.4 Implications for hominoid evolution

Overall, our results demonstrate how a seasonal foraging strategy focused on woodland tree species in an open habitat could drive high levels of chimpanzee arboreality, including arboreal locomotion and suspensory behaviour. Given the similarities in reconstructed palaeoenvironment (e.g., seasonal savannah-mosaics dominated by grassy woodland; Levin et al., 2008; White et al., 2009; Su and Haile-Selassie, 2022; Peppe et al., 2023; reviewed in Su, 2024) and diet (Ungar and Sponheimer, 2011; Henry et al., 2012; Nelson and Hamilton, 2017; van Casteren et al., 2018) between extant savannah-dwelling chimpanzees and some extinct hominoids, our results can inform hypotheses about the selective pressures hominoids may have faced in an open habitat (but see Latimer and Lovejoy, 1990; Ward, 2002; Ward et al., 2011). Importantly, savannah-mosaic habitats are often associated with small statured trees (<10 m; Cerling et al., 2011; MacLatchy et al., 2023), but Issa Valley woodland foraging trees are often >10 m in height and crown diameter (mean values for umbrella- and upside-down cone-shape trees: height 14 m, crown diameter 13 m). Therefore, a foraging strategy of reaching from the ground, as proposed by Hunt (1994b, 1996) postural feeding hypothesis, or simply climbing into the tree with limited horizontal movement (as implied by Senut et al., 2018), would severely limit foraging opportunities in the terminal branch niche in such large trees. Woodland trees also have, on average, low principal branches (average lowest woodland bough height at Issa is 2.8 m; van Leeuwen, 2019), which may actually limit the duration of vertical climbing bouts, and facilitate exiting the tree using terminal branch behaviours, such as suspension, especially in rugged terrain (e.g., Drummond-Clarke et al., 2024). Suspension and assisted bipedalism would therefore offer practical and energy efficient ways to navigate terminal branches, and exit the tree crown in savannah habitat (Drummond-Clarke et al., 2022, 2024). Combined with our previous findings of a high frequency of suspensory locomotion in open habitat (Drummond-Clarke et al., 2022, 2024), the association of suspensory behaviours with navigating large and open tree crowns bolsters suggestions by Pontzer and Wrangham (2004) that traits important for avoiding falls (e.g., orthograde, multi-limbed behaviours that disperse weight below and/or across multiple branches), rather than vertical climbing efficiency, may be a better measure of locomotor performance (i.e., fitness benefits of morphological traits associated with arboreal locomotor safety rather than efficiency) in early hominins. Recent work placing the early Miocene arboreal ape *Morotopithecus* in open habitat also highlights the implications of our findings on understanding hominoid evolutionary origins (MacLatchy et al., 2023; Peppe et al., 2023). Specifically, our study suggests that foraging in large, open trees with abundant terminal branch food can provide the selective pressures for suspensory behaviour and its associated morphology to evolve.

Additionally, given dental evidence that some early hominins likely consumed hard, arboreal food sources in a savannah-mosaic (see Levin, 2015; van Casteren et al., 2018), our finding of longer-to-process foods resulting in more time per tree provides a model for how hard (or tough) object foraging could have driven use of the arboreal niche in some early hominins. This is especially relevant given that a dominant woodland genus at Issa, *Brachystegia*, not only generates fruits with hard exocarps, but also is characterised by large and open upside-down cone shaped crowns, and was possibly characteristic of hominoid woodland habitats from the early Miocene (Bonnefille, 2010; Senut, 2021).

Overall, our results inform on the interaction between morphology, ecology, and ape behaviour in a savannah-mosaic, and have important implications for the interpretation of fossil hominoid behaviour from morphology in analogous environments. Whilst more fossils (especially of African apes) and long-term comparative data will be vital to further test the selective pressures defining ape positional behaviour in a savannah-mosaic, we suggest that interpretations of positional behaviour from morphology of fossil hominoids that lived in an open habitat should not discount the use of suspensory behaviour. If Issa Valley chimpanzees can be considered suitable models, diverse orthograde locomotor behaviours, including suspension, were likely vital for a large-bodied ape to forage effectively, and ultimately survive, in an open habitat.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by the Tanzania Wildlife Research Institute (TAWIRI) and the Tanzania Commission for Science and Technology (COSTECH), and adheres to guidelines laid out by the International Union for Conservation of Nature (IUCN) Primate Specialist Group Section for Human-Primate Interactions, as well as the American Society of Primatologists' principles for ethical treatment of nonhuman primates. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

RD-C: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. SR: Data curation, Investigation, Methodology, Writing – review & editing. FS: Conceptualization, Project administration, Resources, Writing – review & editing. AP: Conceptualization, Project administration, Resources, Supervision, Writing – review & editing.

TK: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

Author SR was employed by GMERC Ltd. Authors FS and AP were founders of GMERC Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1561078/full#supplementary-material

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