Boesch, C, Kalan, AK, Mundry, R, Arandjelovic, M, Pika, S, Dieguez, P, Ayuk Ayimisin, E, Barciela, A, Coupland, C, Ebot Egbe, V, Eno-Nku, M, Fay, JM, Fine, D, Hernandez Aguilar, RA, Hermans,, V, Kadam, P, Kambi, M, Llana, M, Maretti, G, Morgan, D, Murai, M, Neil, E, Nicholl, S, Ormsby, LJ, Orume, R, Pacheco, L, Piel, AK, Sanz, C, Sciaky, L, Stewart, FA, Tagg, N, Wessling, EG, Willie, J and Kühl, HS

Chimpanzee Ethnography Reveals Unexpected Cultural Diversity

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Abstract

Human ethnographic knowledge covers hundreds of societies, whereas chimpanzee ethnography encompasses at most 15 communities. Using termite fishing as a window into the richness of chimpanzee cultural diversity, we address a potential sampling bias with 39 additional communities across Africa. Previously, termite fishing was known from eight locations with two distinguishable techniques observed in only two communities. Here, we add nine previously unstudied termite-fishing communities revealing 38 different technical elements as well as community-specific combinations of three to seven elements. Thirty of those were not ecologically constrained, permitting the investigation of chimpanzee termite fishing culture. The number and combination of elements shared among individuals were more similar within than between communities, thus supporting community-majority conformity via social imitation. The variation in community-specific combinations of elements parallels cultural diversity in human greeting norms or chopstick etiquette. We suggest that termite fishing in wild chimpanzees shows some elements of cumulative cultural diversity.

Introduction

Comparative cultural studies are hampered by the fact that humans are by far the most intensively studied species with many hundreds of well-known different societies[1-2], while non-human species are mostly known from a few populations reaching one dozen in the second most studied species, the chimpanzee[3,4]. Notwithstanding, chimpanzee cultural abilities have been proposed to be limited to simple elements that could be invented independently by each individual performing a given technique[5-7]. Multiple captive studies with chimpanzees and other animal species tend to support this conclusion, and suggest that culture, if present, is not based on a faithful learning mechanism nor any form of teaching, limiting it to simple elements[5-7].

Studies on chimpanzee communities have frequently revealed undocumented behavioral variants for the species, such as algae fishing, accumulative stone throwing, water dipping, cave use, or sequential tool use [8-12]. Additionally, recent research on neighboring chimpanzee communities has revealed the persistence of cultural differences within the same environment[13,14]. Both suggest that incomplete sampling could lead to underestimated chimpanzee cultural complexity[4]. In an attempt to overcome this limitation, we launched a large-scale cross-sectional study with the aim of sampling additional chimpanzee communities for addressing questions about cultural complexity and their potential ecological and social drivers[15]. Here, we present a detailed ethnographic analysis of chimpanzee termite fishing observed at 10 communities, with the three following goals: 1) document the technical elements used by chimpanzees when extracting termites living in a) aerial (epigeal), and b) underground mounds, 2) test whether community-specific techniques are present, and if so 3) assess inasmuch these community-specific techniques could represent a case of cumulative cultural evolution. Given that we investigated variation in the termite-fishing techniques of chimpanzees, any evidence for conformity (i.e., a pattern of within-group homogeneity), in the absence of ecological constraints, would support process-oriented imitation rather than end-state emulation or trial and error learning[5,16] since termite extraction was successful in all instances.

We collected a total of 1,463 one-minute camera-trap videos of chimpanzee termite fishing from 10 communities (range: 14 to 184 for aerial termite fishing; 60 to 336 for underground termite fishing). These videos were analyzed by CB, who has over 40 years' experience observing wild chimpanzees. The termite-fishing ethogram describing individual technical elements was created by CB was tested for reliability with SP, an expert on great ape gestures, on a randomly chosen 10% of videos (N=169) from all 10 termite-fishing communities without SP knowing the community nor the element distribution between communities. Inter-observer agreement in the classification of termite-fishing behaviours was 85% for technical elements, 90% for body part(s) used to fish, 100% for body part(s) used for support and 64% for position of the wrist (Cohen's Kappa test: all $p<0.001$). In addition, two additional independent observers blind to the aim and hypothesis of the study, naïve to the ethogram, and to the origin of the videos, coded the same videos with an average inter-observer agreement of 93% (average Kappa=0.657; N=31 technical elements, with a Kappa higher than 0.8 for 11 of them and 30 out of 31 Kappa values reaching significance at p<= 0.05; N=73 videos). An open-access video library demonstrates the variation in the technical elements coded for termite-fishing behaviour for the different chimpanzee communities (see www.eva.mpg.de/primat/staff/boesch/termite-fishing-video-library.html). For all elements identified, we further inferred whether the element could potentially be explained as the chimpanzees' response to ecological challenges presented by the termite mound structure, and if it was not, we assumed differences reflect social preferences (see Supplementary Table 3 for details).

Results

Aerial termite fishing

Aerial termite-fishing requires an individual to insert one thin twig into a tunnel, deep enough into the termite mound for the soldiers to bite[17]. We discovered chimpanzees of three previously unstudied communities performing this technique (Figures 1). In total, we distinguished 17 different elements for aerial termite fishing, of which 14 were inferred to be primarily socially transmitted, as no ecological constraints could be identified to explain the differences (N=476 videos providing 85 independent sequences of termite fishing including 116 individuals). There were strong community differences in the combinations of elements observed in the majority of individuals within a community (Figure 1; Supplementary Table 1).

Underground termite fishing

Underground termite-fishing involves the use of a tool-set comprising two different-sized sticks: a thick one to perforate (or puncture) the ground to gain access into the mound and a thinner one inserted into the tunnel made by the perforator to fish for termite soldiers[10]. We discovered three previously unstudied chimpanzee communities performing this technique, all located in Central Africa (Figure 2). We observed 21 different technical elements in some, or only one, community (N=987 videos from 107 independent sequences including 132 individuals; Supplementary Table 2). We found strong community differences in the combinations of elements observed in the majority of individuals within a community (Figure 2), and 16 of these elements were inferred to be social preferences.

Testing for group-specific combinations in termite fishing

To investigate whether the combinations of elements observed for termite fishing (Figures 1 and 2) were community specific, we first tested whether the frequency of occurrence of technical elements was community specific, and second, whether individuals from the same community shared more elements than with individuals from different communities. Using a Generalized Linear Mixed Model, we found that individuals shared significantly more elements within a community than with individuals from other communities (permutation test of the contribution of the combination of community and technical elements for aerial nests: standard deviation, sd=3.28, 95% confidence interval (CI): 2.358 to 4.040, P=0.001; underground nests: sd=11.87, CI: 13.157 to 23.468, P=0.001; Figure 3). As seen in Figure 3, some elements were community specific differentiating them from others, such as ‘lean elbow’, which was, only detected in Korup chimpanzees, while ‘lay side’ was specific to the Wonga Wongue chimpanzees. At the other extreme, ‘bite’ or ‘scratch’ occurred in all communities but with different frequencies. Repeating the analysis by permuting mounds rather than individuals did not substantially affect the result (aerial nests: sd=3.21, CI: 2.253 to 4.163, P=0.003; underground nests: sd=10.97, CI: 12.336 to 22.599, P=0.001). The combination of elements exhibited by an individual was also significantly more similar to those of other individuals of the same community, compared with those of other communities (Sørensen similarity index considering only the putatively socially driven elements, leaving 14 elements for the aerial and 16 for the underground data: average similarity of combinations: aerial, different communities: 0.453, different individuals from the same community: 0.741, difference (CI): 0.289 (0.215 to 0.364); underground, different communities: 0.244, different individuals from the same community: 0.873, difference: 0.629 (0.495 to 0.739); both P=0.001; Figure 4a). The fishing technique of the Korup chimpanzees was uniquely characterized by always including 'perfore 1h', 'lean elbow', 'lip shake', 'near elbow' and 'head eat', while in Goualougo chimpanzees the 'long stick' is always combined with 'sit' and 'support 2h', and in the majority, with 'perfore 2h'. Meanwhile the La Belgique chimpanzees combine 'perfore 1h' always with 'long brush' and 'wrist eat' (Figure 3). Finally, a cultural fixation analysis[18] confirmed that elements where alternative elements are present clearly deviated from a random distribution (Figure 4c) with some technical elements showing a strong signal of cultural fixation (group 8 and 11 for underground termite fishing in Supplementary Table 3), and others with more moderate separations between communities (group 2, 4 and 6 in Supplementary Table 3).

Discussion

By carrying out an unprecedented ethnographic analysis of one of the best-studied chimpanzee cultural traits — termite fishing — we show that chimpanzee cultural diversity is currently underestimated due to an under-sampling of different populations. By studying additional communities, we have increased our knowledge about termite-fishing variation from two to 38 elements found in 10 communities. Our results emphasize that community specificity in termite fishing is not only about the absence or presence of elements, but also about the combinations of different elements in each community (Figures 1 and 2). This adds a completely new dimension to the characterization of chimpanzee cultures.

We found that the combinations of elements form community-specific techniques in termite fishing resembled a process of cumulative cultural evolution[7,19,20]. As our study was cross-sectional rather than longitudinal, we do not have historical records to reconstruct the order of invention and inclusion of those elements over time, nor whether they were invented by one or many individuals (but see[21,22] for such evidence in other nonhuman animals). However, given the community specificity of the combinations of elements, when alternatives are present within communities, our results are best explained by a high-fidelity social learning mechanism. The mound structure of the most commonly consumed *Macrotermes* sp. varies extensively depending on the local microclimatic conditions[23,24] and would thus not explain the community-specific distribution of elements. This suggests that in chimpanzees, social influences were stronger than ecological ones.

Although some scholars argue that the accumulation of elements should lead to successive improvements in the cultural trait[7], others recognize that this improvement can also manifest itself in social improvements, comfort or well-being, which remain difficult to measure[19]. For example, in our study, comfort may have driven the variation across communities of chimpanzees lying, sitting or leaning whilst termite fishing (Supplementary Table 1 and 2). Thus, at present, our observations are compatible with accumulated culture (sensu Dean et al.[20]), while a conclusion about true cumulative culture would require data on fishing efficiency being improved by the combinations of elements. The observation that potentially ecologically-dependent technical elements were distributed more widely across communities than socially inferred ones (Supplementary Table 1 and 2) reinforces the suggestion that social transmission is accompanied by a faithful copying mechanism, such as process-oriented imitation[5], while the response to environmental challenges may be supported by more individual learning mechanisms[7].

The present study is not without limitations. Due to the methodology used, we could only record spatially fixed behaviours. This led us to underestimate technical elements that occurred outside the field of view of the camera, or when individuals were positioned behind the mound or with their back towards the camera. While this may not affect the assessment of cultural diversity whenever we had a large number of videos for a community, this was not the case for Bafing, Kayan and Campo Ma'an. Therefore, we may still underestimate cultural diversity in chimpanzee termite fishing.

Limited population sampling has biased our knowledge of chimpanzee culture, preventing us from fully understanding human cultural uniqueness. We showed that chimpanzees have a larger termite-fishing diversity than previously assumed. More importantly, our findings suggest that 'chimpanzee etiquette', similar to human forms of etiquette[25,26], is likely based on a high-fidelity social transmission mechanism among individuals of a population, resulting in an accumulation of community-specific elements. Therefore, this study notably decreases the gap between chimpanzee and human cultural abilities.

Methods

This study uses non-invasive behavioural observations collected on wild chimpanzees as part of the Pan African Programme: The Cultured Chimpanzee ('PanAf'). All field research complied with the ethical regulations and standards set by the relevant government authorities present within each host country (see Acknowledgements for full list of governmental bodies that provided authorizations for this study). Moreover, no experiments on animals were conducted therefore randomization of experimental protocols was not necessary. The sampling strategy for the PanAf was to conduct a minimum of 1 year of fieldwork on wild chimpanzee communities that were unknown or poorly known behaviourally to scientists to better capture the variation present in this species. The communities were selected following different criteria: 1) a balanced number of communities for each African region, 2) a balanced representation of the main ecosystems inhabited by chimpanzees, 3) previous information on the presence of chimpanzees available for the site, and 4) sufficient security for our field teams. After 8 years of collecting data at 46 chimpanzee communities across the species range, for a range of 1-30 months, we observed 10 communities termite fishing, 1 of which was already known to do so (Goualougo). The study examined termite fishing camera-trap videos collected via the PanAf from all 10 communities. Individual chimpanzees were identified both within and across each termite fishing sequence (i.e., across multiple videos). As in previous studies on chimpanzee tool-use using camera-trap data[9], individuals were identified using a combination of sexual characteristics, facial features, and conspicuous markings or injuries.

Ecological versus socially inferred behavioural elements

To distinguish whether a technical element is primarily socially or ecologically driven, we used the following two definitions: a technical element for which the chimpanzee had different alternatives which are not constrained by ecological parameters was defined to be driven by social factors. In Supplementary Table 3, the alternative elements are identified by similarly numbered groups. On the other hand, a technical element that was obviously ecologically constrained was defined to be driven by ecological factors (Supplementary Table 3). Examples of ecological constraints include the structure and depth of the termite mound that could affect stick length, the hardness of the soil that could affect perforation technique, or the availability of raw material that could affect stick rigidity[27]. Detailed studies on the architecture of the *Macrotermes bellicosus* mounds, the most-often fished species by chimpanzees, revealed extensive variability within the same local area due to specific microclimatic conditions[23,24]. Still, some ecological aspects could partly affect the use of other technical elements, however we classified them as social as long as we observed that chimpanzees possess alternative elements with which they can respond. For example, the defensive behaviour of the termites could affect the stick shaking movements, but since chimpanzees shake the stick in different ways, we classified these elements as being socially driven (group 3 in Supplementary Table 3). Similarly, the termites may bite with differing efficiency at a stick with different ends, but since chimpanzees were seen to make small and long brushes, and bite or peel the extremity we classified these elements as being socially driven (group 5 and 9 in Supplementary Table 3).

Inter-observer Reliability

In order to determine reliability, two raters independently coded 23 technical elements (Christophe Boesch and Simone Pika, and later Julia Riedel and Isabel Ordaz Németh). We only included in the final analyses elements that occurred at a minimum of eight times across different communities and videos. We then measured reliability using Cohen's Kappa[28], separately for behaviour, body part, supporting position, body part supporting, and, wrist position. For each of these, we determined Kappa twice, once considering cases in which the second rater did not see an element noted by the first rater as a mismatch, and once excluding such cases. We further evaluated reliability on the level of the individual behavioural elements using a one-tailed binomial test. To this end, we counted the number of times the second rater coded the same behaviour as the first one. We then set the expected proportion of chance agreement to the product of the numbers of times both raters coded the behaviour in question, divided by the squared total of coded behaviours. As before, we applied this approach twice, once considering the cases, in which the second rater did not see an element as a mismatch, and once excluding such cases. Details for the agreement between CB and SP are provided in Supplementary Tables 4 and 5.

Statistical analysis

Distribution of different technical elements across communities

As overall tests of whether the occurrence of technical elements was community specific, we fitted two Generalized Linear Mixed Models (GLMM)[29] with binomial error structure and logit link function[30], one for the aerial termite data and one for the underground termite data. Into these, we included, besides the intercept as the sole fixed effect, random intercepts for the community, the mound, the individual, the technical element, and the combination of community and technical element. This latter random intercept accounts for community-specific preferences for the utilization of technical elements. Furthermore, to account for varying observation times per combination of individual and mound, we included it (log-transformed) as an offset term into the model[30]. Since tests of random effects are somewhat problematic[31], and since the elements were in part mutually exclusive, we decided to conduct a permutation test[32] of whether the random intercept of the combination of community and technical element significantly contributed to explaining the response. To this end, we randomized the assignment of individuals to communities. We conducted 1,000 permutations into which we included the original data as one permutation. As the test statistic, we chose the estimated variance (precisely the standard deviation) in the response attributed to variation among the levels of the random effect of the combination of community and technical element. We determined the P-value as the proportion of permutations revealing a test statistic at least as large as that of the original data. We indicate model estimates (standard deviations associated with the random intercepts effect of the combination of community and technical element) as a measure of effect size and determined their 95% confidence intervals by means of a parametric bootstrap (N=1,000). The models were fitted in R (version 3.4.4)[33] using the function glmer of the package lme4 (version 1.1-17)[34], and we bootstrapped model estimates using the function bootMer of the same package. The sample sizes for aerial nests in these models were 1546 total presences/absences (comprising 517 presences) of 17 technical elements for 71 individuals from five communities, observed at 23 mounds, and 85 combinations of community and technical elements. For underground nests, the data included 1788 total presences/absences (comprising 490 presences) of 21 technical techniques for 90 individuals from six communities and comprising 120 combinations of community and technical elements. From both data sets, we dropped combinations of individual and technical elements for which we could not reliably code the presence or absence of the behaviour.

However, potential differences between communities could also be largely driven by specificities of the particular mounds rather than individual preferences differing systematically between communities. We hence decided to run an additional permutation test in which we randomly shuffled the assignment of communities (and their individual members) among termite mounds.

Since a few individuals had been observed at several different termite mounds, creating complications regarding the random assignment of communities to mounds, we excluded them from this analysis. Hence, this analysis is more conservative due to a smaller sample size in terms of the number individuals included in combination with fewer units (i.e., mounds rather than individuals) being permuted. The sample sizes for these models were 1,064 total presences/absences (comprising 350 presences) of 17 technical elements for 62 individuals from five communities observed at 13 mounds, and comprising 85 combinations of community and technical elements (aerial mounds) and 1,200 total presences/absences (comprising 324 presences) of technical elements for 77 individuals from six communities observed at 29 mounds, and comprising 119 combinations of community and technical elements (underground mounds).

Sharing of technical elements within compared to across communities

To estimate whether individuals belonging to the same community shared more technical elements than individuals belonging to different communities, we measured the dyad-wise overlap between combinations of individuals by means of Sørensen's similarity index[35]. This is calculated as follows:

$$\text{Sørensen}_{i,j} = 2 \times N_{sharedPres} / (2 \times N_{sharedPres} + N_{only\ i} + N_{only\ j})$$

where $N_{sharedPres}$ is the number of technical elements present in both individuals *i* and *j*, and $N_{only\ i}$ and $N_{only\ j}$ are the number of technical elements observed only in individual *i* and *j*, respectively. It is worth noting that Sørensen's index considers only technical elements present in at least one of the two individuals of a given dyad.

We tested whether individuals of the same community shared on average more technical elements than individuals of different communities by means of a Mantel like permutation test[36], which permuted the individuals across communities. As a test statistic, we used the absolute difference between the average similarity indices between individuals of the same and different communities, respectively. We conducted 1,000 permutations into which we included the original data as one permutation and determined the P-value as the proportion of permutations revealing a test statistic at least as large as that of the original data. We conducted this test twice, separately for the aerial and underground nest data (Figure 4a and b, respectively). As a measure of effect size we indicate the difference between the mean similarity indices between individuals of the same and different populations. We determined the 95% confidence interval of this measure by means of a non-parametric bootstrap (N=1,000), sampling the individuals. Since the individuals contributed differing numbers of sequences to the data, the bootstrapped data sets usually differed from the original one in terms of the number of sequences. For these analyses, we considered only those individuals for which all the behaviour elements considered in a data set (aerial or underground, respectively) could be reliably coded. Hence, the sample sizes for these analyses are smaller than for the models described above, namely a total 877 absences and 371 presences observed for 86 sequences of 60 individuals (aerial data) and 991 absences and 311 presences observed for 100 sequences of 68 individuals (underground data).

Calculating the cultural fixation index

To compare the proportion of variation in technical elements exhibited within and between populations, we calculated a cultural F_{ST}. Cultural F_{ST} is negatively correlated with within-group similarity, meaning higher F_{ST} values reflect more between group differences than within. We used an approach similar to Bell and colleagues[18] but with a modification since the original method leads to F_{ST} values larger than 1 in highly differentiated populations. This modified cultural F_{ST} method was originally developed by Handley and Mathew[37] to account for variation in sample size and populations having unique traits specific to them. We calculated the F_{ST} separately for each group of putatively socially driven technical elements and also separately for aerial and underground nests. In order to determine cultural F_{ST} values we processed the data as follows. In a first step, we determined for each sequence of each individual which element of a given group of mutually exclusive elements it had used (see Supplementary Table 3 and Supplementary Data 7 for details of the F_{ST} calculation). This led to two matrices (one for aerial and one for underground nests), each with one row per sequence and one column for each group of mutually exclusive elements. Since some groups of mutually exclusive elements rarely occurred (when more than 50% of the sequences did not have an entry for the respective group), we excluded them from the data and subsequently excluded all sequences in which for at least one of the remaining groups none of the mutually exclusive elements appeared. This subsetting of the data aimed at using the same sample size per each element of a given group of mutually exclusive patterns when calculating the cultural F_{ST}. The final sample for the aerial data consisted of 80 sequences from 53 individuals out of five communities with behaviours from three groups (2, 4, and 6) of mutually exclusive technical elements, and the final sample for the underground data consisted of 78 sequences from 58 individuals out of six communities with behaviours from two groups (8 and 11) of mutually exclusive technical elements. Since some of the individuals varied with regard to which particular element of a group of mutually exclusive elements they used in a given sequence, we then randomly selected one sequence per individual (generating a population of 'haploid' individuals) and then determined the cultural F_{ST} for each group of mutually exclusive elements. In order to remove the effects of any particular random selection, we repeated this 1,000 times and report average results and their variation (Figure 4c). F_{ST} values were small in group 2, 4, and 6 and comparatively large in group 8 and 11 (Figure 4c). Furthermore, particularly within group 4 and 11, F_{ST} values varied considerably between different random selections of technical elements per individual.

Data Availability

The data for this study have been uploaded as part of the supplementary files (Supplementary Data 1-6).

Code Availability

The custom code used for all statistical analyses has been uploaded as part of the supplementary files (Supplementary Data 7 and 8).

References

1- Collard, I. and Foley, R. Latitudinal patterns and environmental determinants of recent human cultural diversity: do humans follow biogeographical rules? *Evolutionary Ecology Research*, **4**, 371-383 (2002).

2- Foley, R. and Lahr, M. On Stony Ground: Lithic Technology, Human Evolution, and the Emergence of Culture. *Evolutionary Anthropology*, **12**, 109-122 (2003).

3- Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C., Wrangham, R. and Boesch, C. Cultures in chimpanzee. *Nature*, **399**, 682-685 (1999).

4- Boesch, C. *Wild Cultures: A Comparison Between Chimpanzee and Human Cultures*. Cambridge: Cambridge University Press (2012).

5- Tomasello, M. *The Cultural Origin of Human Cognition.* Cambridge: Harvard University Press (1999).

6- Galef, B. Approaches to the study of traditional behaviors of free-living animals. *Animal Learning and Behavior*, **32 (1)**, 53–61 (2004).

7- Tennie, C., Call. J. and Tomasello, M. Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B*, **364**, 2405-2415 (2009).

8- Kühl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F. D'Auvergne, L. et al. Chimpanzee accumulative stone throwing. *Sci. Rep.* **6**, 22219 (2016).

9- Boesch, C., Kalan, A.K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V. & Kühl, H.S. Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *Am. J. Primatol.* **79**, 1–7 (2017).

10- Sanz, C., Morgan, D. and Gulick, S. New Insights into Chimpanzees, Tools, and Termites from the Congo Basin. *Am. Nat.* **164(5)**, 567-581 (2004).

11- Lapuente, J., Hicks, C. and Linsenmair, E. Fluid dipping technology of chimpanzees in Comoé National Park, Ivory Coast. *Am. J. Primatol.*, **79**, e22628 (2017).

12- Pruetz, J. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. Implications for thermoregulatory behavior. *Primates*, **48**, 316-319 (2007).

13- Luncz, L., Mundry, R. and Boesch, C. Evidence for cultural differences between neighboring chimpanzee communities. *Curr. Biol*. **22**, 922-926 (2012).

14- Pascual-Garrido, A. Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. *Sci. Rep.* **9**, 8260 (2019).

15- Kühl, H., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M. et al. Human impact erodes chimpanzee behavioral diversity. *Science*, **363 (6434)**, 1453-1455 (2019).

16- Caldwell, C., Schillinger, K., Evans, C. and Hopper, C. End state copying by humans (Homo sapiens): implications for a comparative perspective on cumulative culture. *J. Comp. Psych*. **126(2)**, 161-169 (2012)

17- Goodall, J. Behaviour of free-living chimpanzees of the Gombe Stream area. *Anim. Behav. Monogr.* **1**, 163-311 (1968).

18- Bell, A., Richerson, P. and McElreath, R. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *PNAS*. **106**, 17671-17674 (2009).

19- Mesoudi, A. and Thornton, A. What is cumulative cultural evolution? *Proc. R. Soc. B,* **285**, 20180712 (2018).

20- Dean, L., Vale, G., Laland. K., Flynn, E. & Kendal, R. Human cumulative culture: a comparative perspective. *Biol. Rev.*, **89**, 284-301 (2014).

21- Schofield, D., McGrew, W., Takahashi, A. and Hirata, S. Cumulative culture in nonhumans: overlooked findings from Japanese monkeys? *Primates*, **59**, 113-122 (2018).

22- Hunt, G. and Gray, R. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. B*, **270**, 867-874 (2003).

23- Korb, J. Termite mound architecture, from function to construction. In *Biology of Termites: A Modern Synthesis* (Eds. Bignell, D., Roisin, Y. and Lo, N.), pp. 349-373. New York: Springer (2011).

24- Korb, J. and Linsenmair K. 1998. The effect of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. Insectes Sociaux, **45(1)**, 51-65.

25- Wang, E. Q. *Chopsticks: A Cultural and Culinary History*. Cambridge, Cambridge University Press (2015).

26- Firth, R. Verbal and bodily rituals of greeting and parting. In *The Interpretation of Ritual* (Ed. Fontaine, J.S.). Pp: 1-38. London: Routledge Library Editions (1972).

27- Sanz, C., Deblauwe, I., Tagg, N. and Morgan, D. Insect prey characteristics affecting regional variation in chimpanzee tool use. *J. Hum. Evol.* **71**, 28-37 (2014).

28- Siegel, S. & Castellan, N.J.Jr. *Nonparametric statistics for the behavioral sciences (2nd ed.)*. New York, NY, England: Mcgraw-Hill Book Company (1988).

29- Baayen, R.H. *Analyzing Linguistic Data*. Cambridge: Cambridge University Press (2008).

30- McCullagh, P. & Nelder, J.A. *Generalized linear models*. London: Chapman and Hall (1989).

31- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., et al. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol*, **24**, 127-135 (2009).

32- Adams, D.C. & Anthony, C.D. Using randomisation techniques to analyse behavioural data. *Anim. Behav*. **51**, 733–738 (1996).

33- R Core Team. R: *A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna, Austria (2018).

34- Bates, B., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Soft*. **67**, 1-48 (2015).

35- Sørensen, T. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskab*, **5**, 1–34 (1948).

36- Sokal, R.R. & Rohlf, F.J. *Biometry - The Principles and Practice of Statistics in Biological Research* (3rd ed.). New York: Freeman & Co. (1995).

37- Handley, C. & Mathew, S. Human large-scale cooperation as a product of competition between cultural groups. *Nature Communications*, **11**, 702 (2020).

38- Humle, T., Maisels, F., Oates, J.F., Plumptre, A. & Williamson, E.A. *Pan troglodytes (errata version published in 2018).* The IUCN Red List of Threatened Species. e.T15933A129038584 (2016).

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Author Contributions

C.B., M.A., and H.S.K., designed the study and oversaw data collection; C.B., M.A., and P.D. compiled data for this study; C.B., R.M., S.P., I.O-N., J.R. and A.K.K. analyzed the data; C.B., R.M. and A.K.K. prepared figures; C.B., A.K.K., M.A. and H.S.K. wrote the manuscript with input from all coauthors. E.A.A., A.B., C.C., V.E.E., J.M.F., D.F., R.A.H.A., V.H., P.K., M.K., M.L., E.N.M., G.M., D.M., M.M., E.N., S.N., L.J.O., R.O., L.P., A.P., C.S., L.S., F. S., N.T., E.G.W., and J.W. collected data in the field.

Competing Interests

The authors declare no competing interests.

Figure Legends

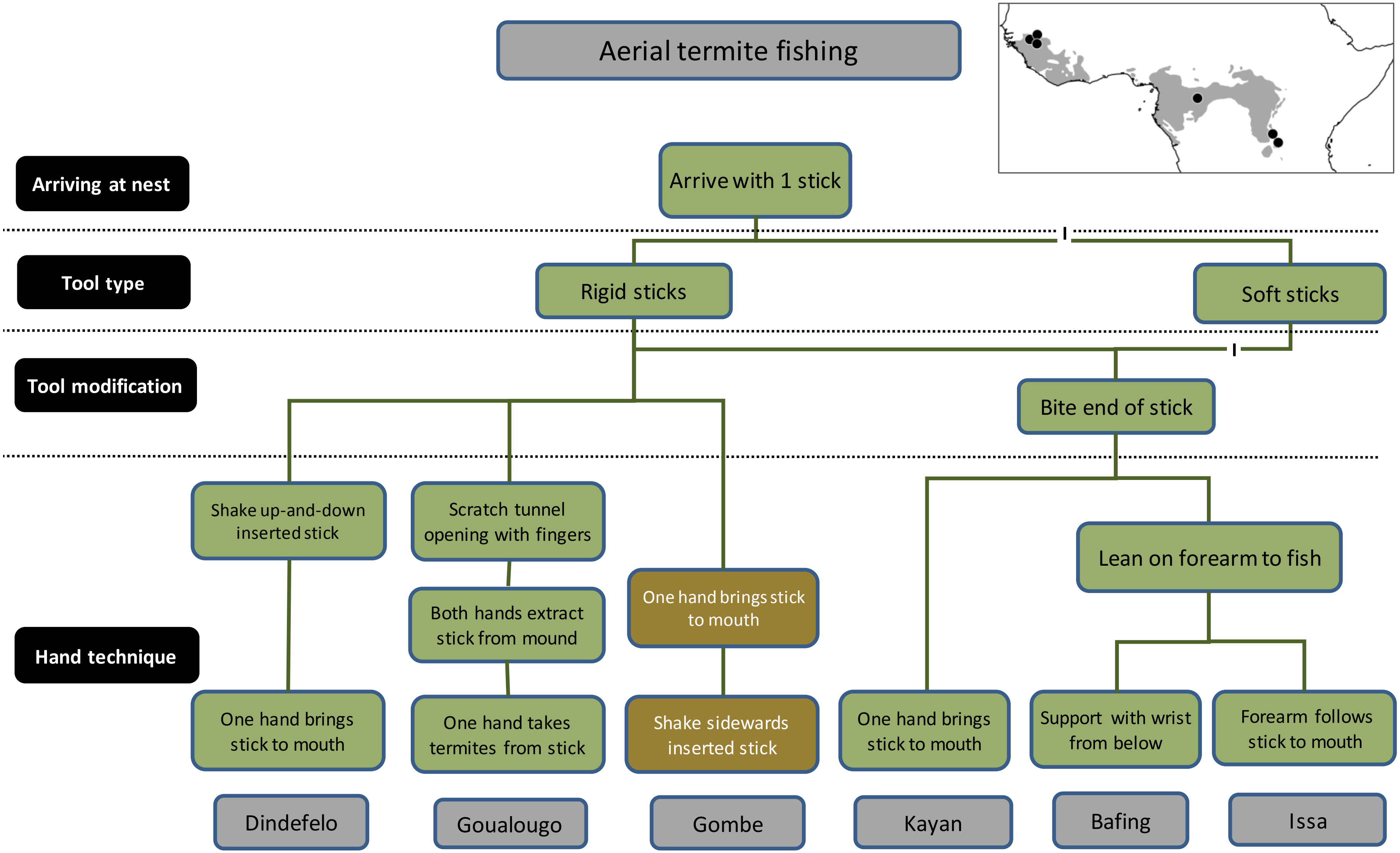
Figure 1: **Cultural diversity when fishing termites from aerial nests in six different chimpanzee communities**.[38] Only elements observed in at least 50% of the individuals of a community and differing between communities are included (Table S1). For Gombe chimpanzee, no quantification is provided (in brown). Each element in a box interconnects with the other elements present within each community and connections do not reflect a hierarchy, but highlight the combinations of elements in each community. The variation in the combinations observed partly reflects different ecological challenges and social preferences (see Table S1), while the number of elements within each community reflects an assumed accumulation process. I=Issa chimpanzees only.

Figure 2: **Cultural diversity when fishing termites from underground nests in six different chimpanzee communities**.[38] Only elements observed in at least 50% of the individuals of a community and differing between communities are included (Table S2). Each element in a box interconnects with the other elements found within each community. Some elements are unique to a community (e.g., "peel the bark" of the stick in La Belgique chimpanzees, or "shake with the lips" the inserted stick in Korup (K) chimpanzees), while others are shared among communities. The connections do not reflect a hierarchical order in performing the technique, but highlight the distinguishing features of the combination of elements in each community. The Goualougo (G) technique is typified by 6 elements, including a unique perforation element as well as elements shared with other communities, "sit to fish" shared with Campo Ma'an, Mont Cristal (MC), and La Belgique, while "pull through teeth to make short brush", "support with two hands" and "insert stick with both hands" are shared with Campo Ma'an and Mont Cristal. WW=Wonga Wongue.

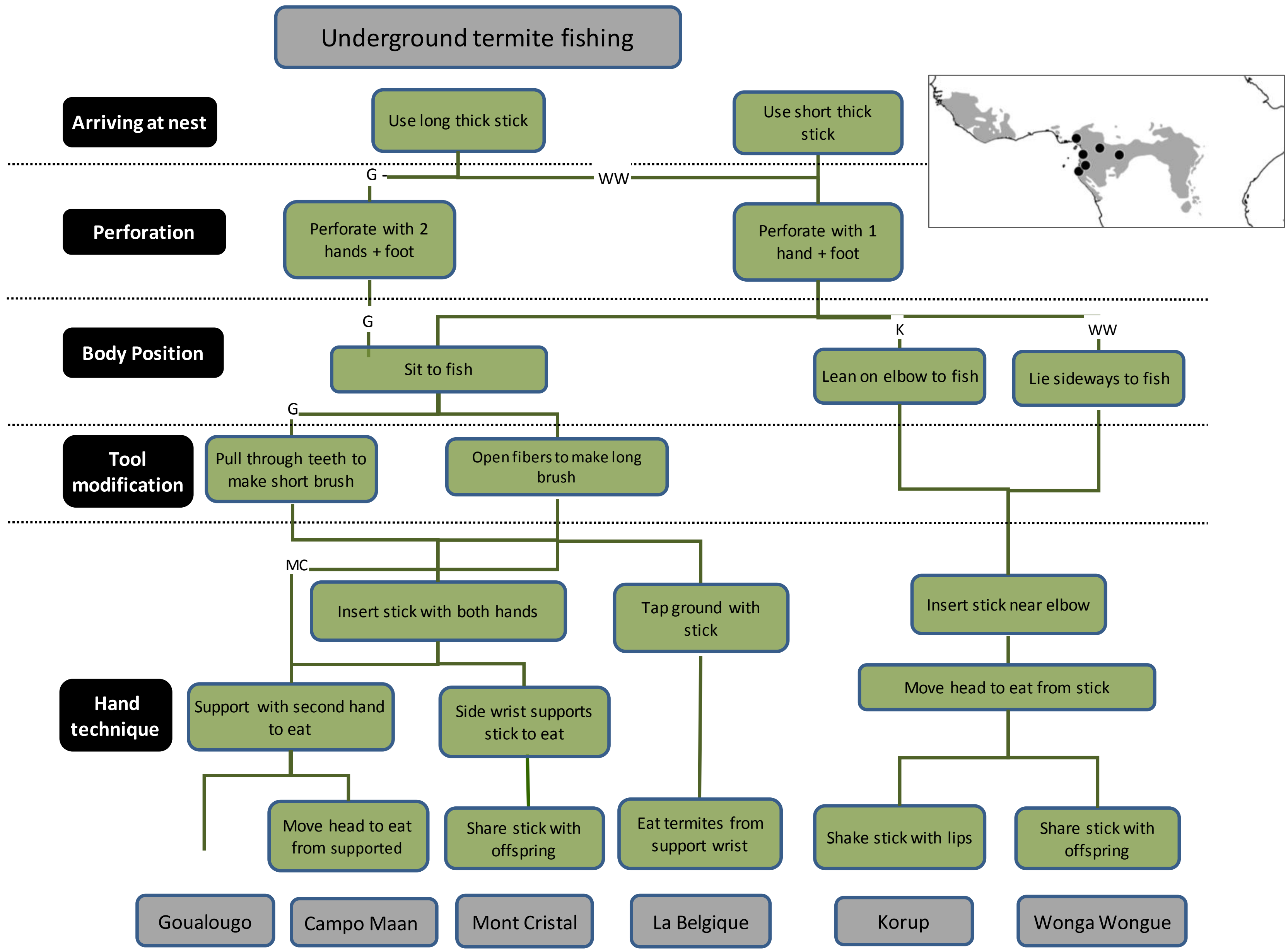
Figure 3: **Occurrence of technical elements in 10 different chimpanzee communities for (a) aerial termite nests and (b) underground termite nests.** The black fraction of the circles depicts the proportion of sequences in which the respective element was present, and the area of the circles depicts the number of sequences observed (range: 1 to 54; variation of sample size within communities is due to occasional missing values that occurred when it could not be reliably seen whether a given element was present in a given sequence). See also Supplementary Table 1 and 2.

Figure 4: **Similarity (Sørensen's similarity index) between combinations of putative social elements only, compared for individuals belonging to different or the same community, for elements observed at (a) aerial and (b) underground nests.** Indicated are medians (thick horizontal lines) quartiles (boxes), and 2.5 and 97.5% quantiles (vertical lines). (**c) Cultural F_{ST} values for five groups of**

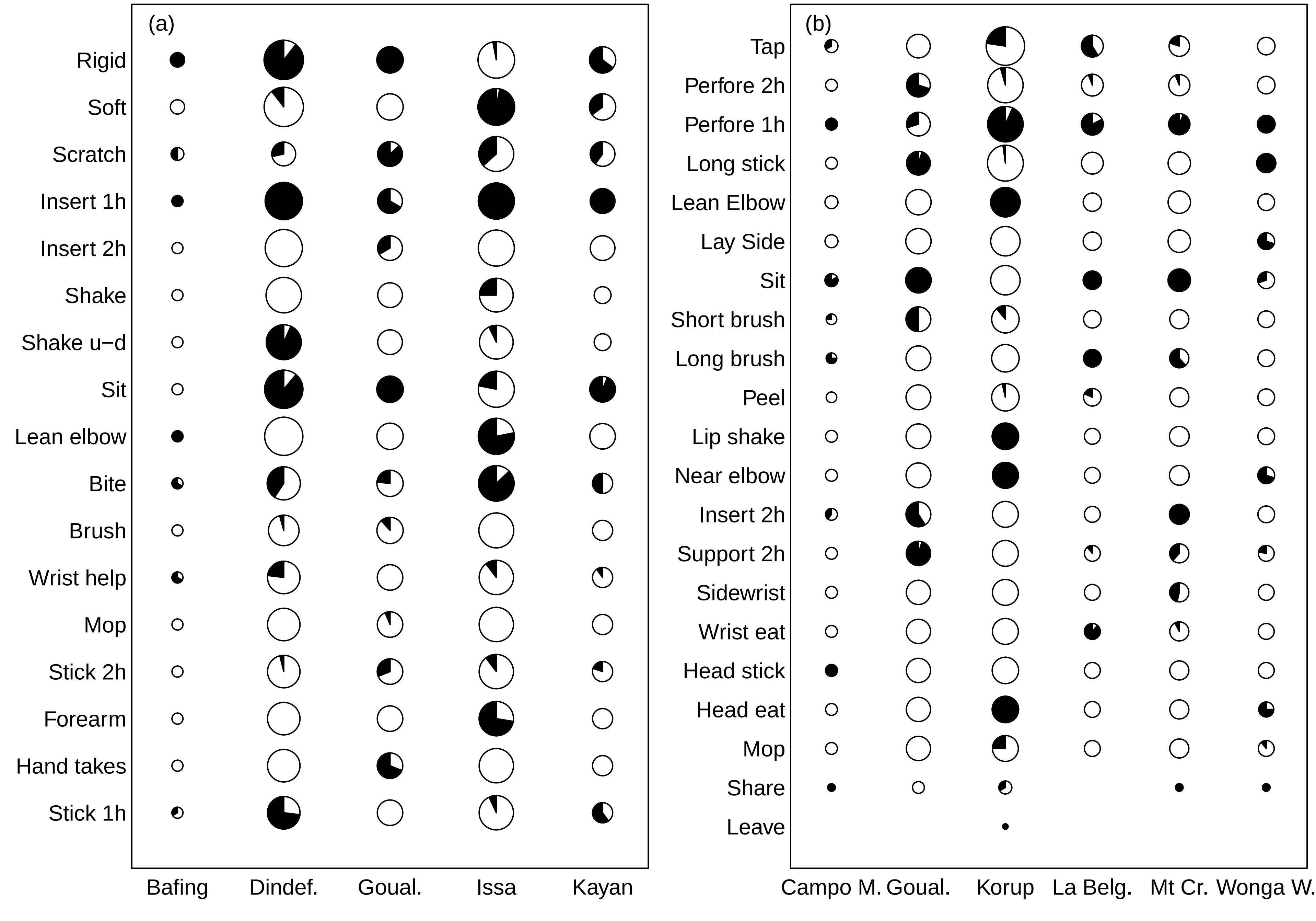
mutually exclusive technical elements (2, 4 and 6 for aerial and 8 and 11 for underground nests, see Supplementary Table 3). Indicated are medians, quartiles, and 2.5 as well as 97.5 quantiles of the F_{ST}-values obtained from different random selection of sequences. F_{ST} values close to 1 indicates complete separation between communities, like for groups 8 and 11, values between 0.1 and 0.4 indicates weaker separations between communities, like for groups 2, 4 and 6.

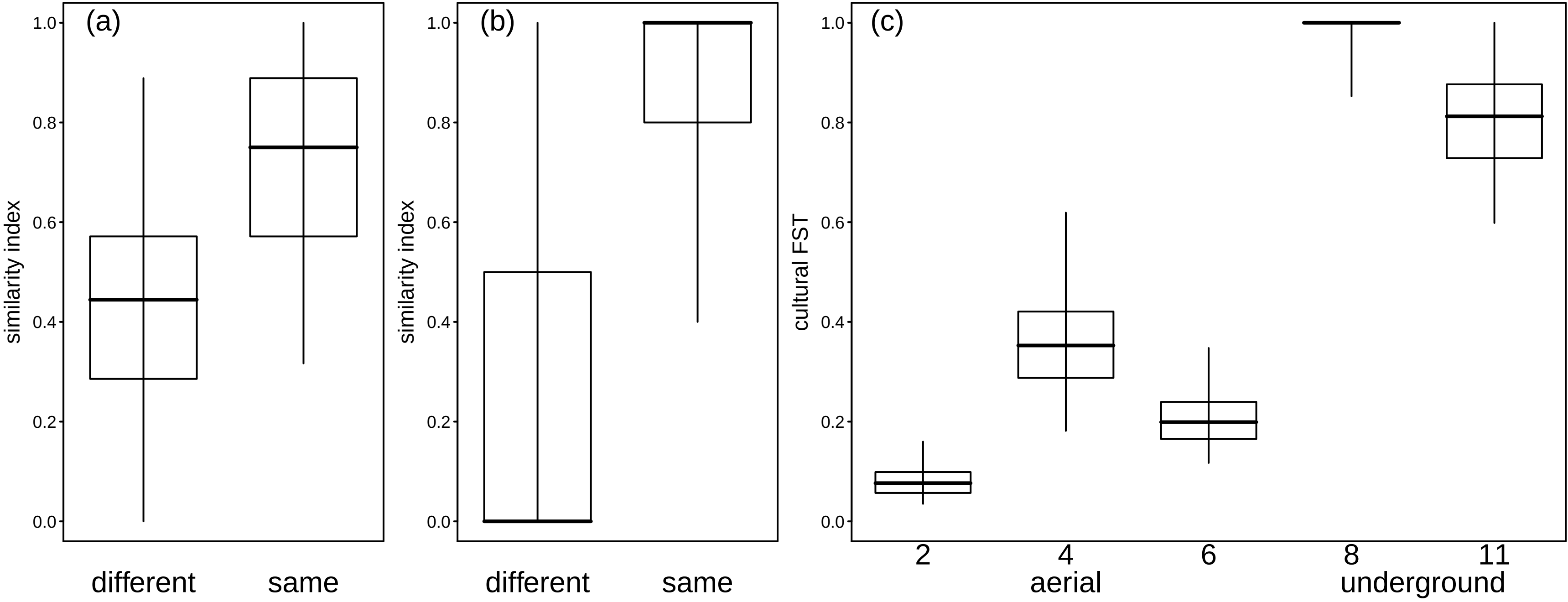


Aerial termite fishing
Arriving at nest
Arrive with 1 stick
Tool type
Rigid sticks
Soft sticks
Tool modification
Bite end of stick
Hand technique
Shake up-and-down inserted stick
Scratch tunnel opening with fingers
Both hands extract stick from mound
One hand brings stick to mouth
Lean on forearm to fish
One hand brings stick to mouth
One hand takes termites from stick
Shake sidewards inserted stick
One hand brings stick to mouth
Support with wrist from below
Forearm follows stick to mouth
Dindefelo
Goualougo
Gombe
Kayan
Bafing
Issa



Underground termite fishing
Arriving at nest
Perforation
Body Position
Tool modification
Hand technique
Use long thick stick
Use short thick stick
G
WW
Perforate with 2 hands + foot
Perforate with 1 hand + foot
G
K
WW
Sit to fish
Lean on elbow to fish
Lie sideways to fish
G
Pull through teeth to make short brush
Open fibers to make long brush
MC
Insert stick with both hands
Tap ground with stick
Insert stick near elbow
Move head to eat from stick
Support with second hand to eat
Side wrist supports stick to eat
Move head to eat from supported
Share stick with offspring
Eat termites from support wrist
Shake stick with lips
Share stick with offspring
Goualougo
Campo Maan
Mont Cristal
La Belgique
Korup
Wonga Wongue


(a)
Rigid
Soft
Scratch
Insert 1h
Insert 2h
Shake
Shake u−d
Sit
Lean elbow
Bite
Brush
Wrist help
Mop
Stick 2h
Forearm
Hand takes
Stick 1h
Bafing
Dindef.
Goual.
Issa
Kayan
(b)
Tap
Perfore 2h
Perfore 1h
Long stick
Lean Elbow
Lay Side
Sit
Short brush
Long brush
Peel
Lip shake
Near elbow
Insert 2h
Support 2h
Sidewrist
Wrist eat
Head stick
Head eat
Mop
Share
Leave
Campo M.
Goual.
Korup
La Belg.
Mt Cr.
Wonga W.



(a)
(b)
(c)
similarity index
similarity index
cultural FST
1.0
0.8
0.6
0.4
0.2
0.0
different
same
different
same
2
4
6
8
11
aerial
underground