

Please see my changes below. trust me that i only do changes that are necessary. Details matter a lot in animal culture. Given that we cannot do a track changes thing in MS word, I trust that you

add these things to the MS or when you dont that you prediscuss omissions with me. Below are the insertions required, in red.

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can you pls draft an abstract?

cultural transmission | cultural evolution | cumulative culture | chimpanzees ~~X~~ culture | individual-based models / animal culture

beliefs from  
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more effective

**\*\* ..and certainly present in all apes**

potential

We built an individual-based model that reproduces a world inhabited by six populations of “oranzees”, a hypothetical ape species. The model is space-explicit: the oranzees populations are located at relative positions analogous to the six chimpanzees sites in (3). This is important to determine the genetic predispositions and ecological availabilities associated to their possible behaviours (see below). Population sizes are also taken from the sites in (3). Following (9), we use data from (10), and we define population sizes as  $N = \{20; 42; 49; 76; 50; 95\}$ .

yet

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XX cite Bandini &amp; Tennie here

into

can you draft one please?

Authors must submit a 120-word maximum statement about the significance of their research paper written at a level understandable to an undergraduate educated scientist outside their field of speciality. The primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad readership. The Significance Statement appears in the paper itself and is required for all research papers.

Please declare any conflict of interest here.

\*because there are other papers, and otherwise it looks like we ignore them.

32 food-related behaviours. These figures were chosen to resemble the behaviours considered in (3).

In the case of social behaviours, we assume four sub-categories, each with eight possible different behaviours, that serve the same goal. Oranzees' state is based on how many of the four goals are fulfilled. A goal is considered fulfilled if an oranzee has at least one behaviour out of the eight in the sub-category. An oranzee has a state value of 0.25 if, for example, it has at least one behaviour among the first eight behaviour, and none of the others, and a state value of 1 if there is at least one behaviour in each sub-category.  $p_{\text{social}}$ , the probability to innovate a social behaviour, is drawn from a normal distribution with mean equal to  $1 - \text{state}_{\text{social}}$ .

Food-related behaviours are analogously divided in sub-categories, with the differences that there is a variable number of behaviours in each sub-category, and that sub-categories are associated to two different 'nutrients',  $Y$  and  $Z$ . The idea is that individuals need to balance their nutritional intake, so that their optimal diet consist in a roughly equal number of food for one and the other nutrient. The state, for food-related behaviours, depends on the total amount of food ingested and on the balance between nutrients, and it is calculated as the sum of each sub-category fulfilled (as above, for this to happen there needs to be at least one behaviour present) minus the difference between the number of sub-categories providing nutrient  $Y$  and the number of sub-categories providing nutrient  $Z$ . We normalize the state between 0 and 1, and, as above  $p_{\text{food}}$  is then calculated as  $1 - \text{state}_{\text{food}}$ . (Further details in SI).

**Socially-mediated reinnovation.** At each time step, all oranzees have a probability of innovation for social and food-related behaviours calculated as described above. The specific behaviour an oranzee will innovate depends both on the frequency of the behaviours already present in the population, and on the ecological availability and genetic propensity associated to the behaviour. A further parameter of the model,  $S$ , controls the probability that each reinnovation is socially-mediated. When a reinnovation is socially-mediated, the probability of innovating each behaviour  $B_i$  is weighted by its proportional instances in the population, among the behaviours of the same category, so that common behaviours are more likely to be reinnovated.

When the reinnovation is not socially-mediated, the probability of innovating each behaviour is random. Only one behaviour per category can be innovated at each time step.

**Genetic propensity and ecological availability.** The behaviour selected in the previous step is then innovated or not according to its genetic propensity and, in case of food-related behaviours, ecological availability.

Genetic propensity is a probability  $p_g(0, 1)$ , assigned independently for each of the 64 behaviours. A parameter of the model,  $\alpha_g$ , determines the probability that the genetic propensity of each behaviour is equal for all the six populations or whether is different.

If it is equal,  $p_g$  is randomly drawn. If it is different, we assign the propensity using a geographical gradient. We choose a random point and calculate its distance to each population. Distances are then transformed to  $p_g$  by rescaling them between 0 and 1, so that for the farther site  $p_g = 0$  i.e. the associated behaviour will be impossible to express

(see SI). Notice that  $\alpha_g = 0$  does not mean that there are no genetic influences on the behaviours, but that there are no differences between the populations with regard to this aspect.

Ecological availability is a probability  $p_e(0, 1)$  that represents the likelihood of finding a resource, or its nutritional value, in each site. Ecological availability is assigned only to food-related behaviours, and it is calculated in the same way of  $p_g$ , using the parameter  $\alpha_e$  to determine the probability of ecological availability being different in the six populations.

**Model's output.** We run simulation for  $t_{\text{max}} = 6000$  (corresponding to 500 years of oranzee-time). For each simulation, following (3), we classify each behaviour, in each population, as:

- *customary*: a behaviour observed in over 50% of individuals in at least one age class (see SI for how age classes are defined in our model).
- *habitual*: a behaviour observed in at least two individuals across the population.
- *present*: a behaviour observed in at least one individual across the population.
- *absent*: a behaviour not observed even once in the population.
- *ecological explanations* is a behaviour that is absent because of complete lacking of local ecological availability (i.e., in our model, associated to  $p_e = 0$ ).

Notice the last category in (3) (*unknown*, i.e. "the behaviour has not been recorded, but this may be due to inadequacy of relevant observational opportunities") does not apply in our case.

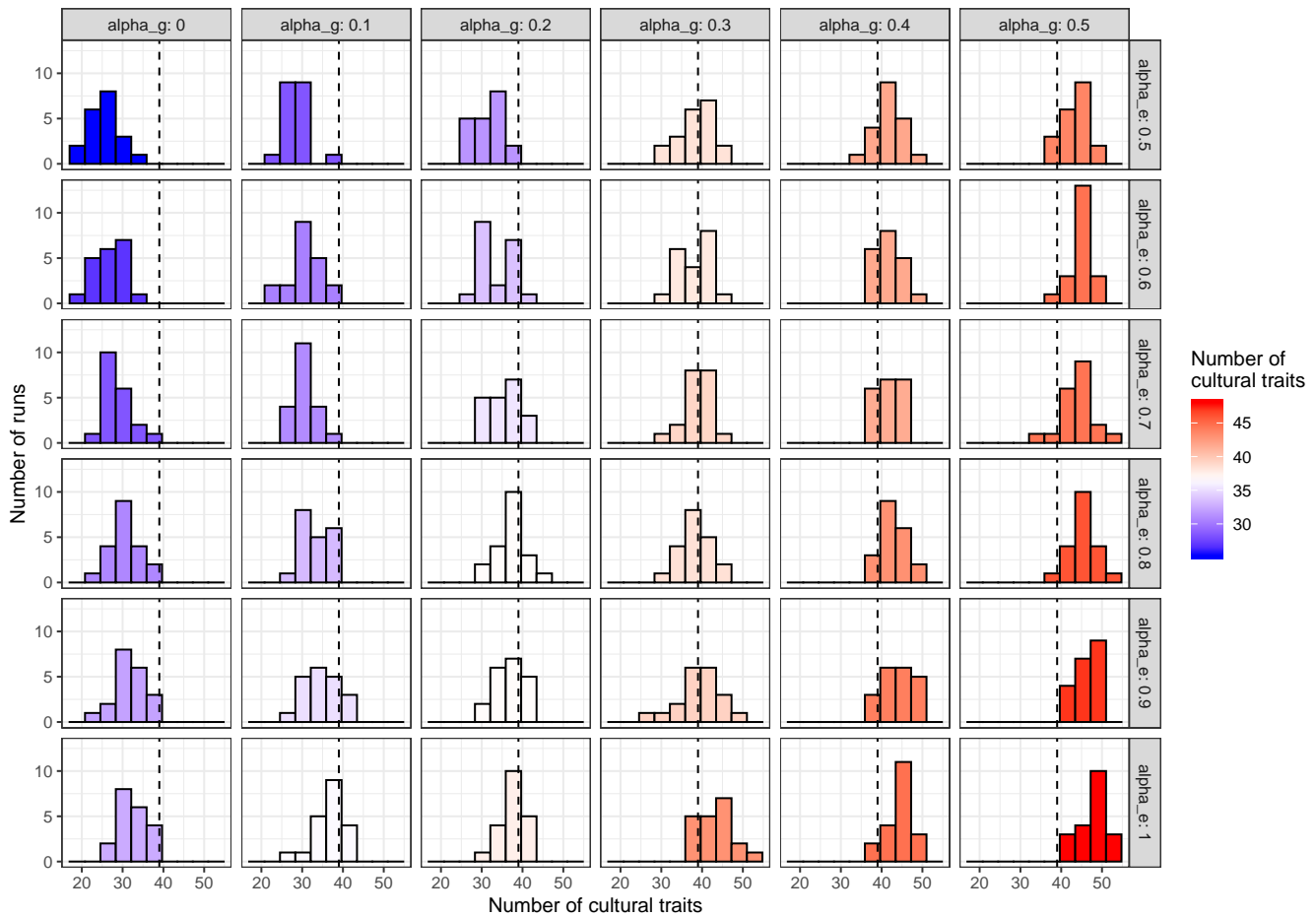
Finally, we calculate the same "patterns" described in (3):

- $A$ : behaviour absent at no site.
- $B$ : behaviour not achieving habitual frequencies at any site.
- $C$ : behaviour for which any absence can be explained by local ecological factors.
- $D$ : behaviour customary or habitual at some sites yet absent at others, with no ecological explanation, i.e. the behaviours defined as "cultural".

## Results

We are particularly interested in the realistic parameter conditions of moderate to high environmental variability ( $\alpha_e = (0.5, 1)$ ) and zero to moderate genetic differences ( $\alpha_g = (0, 0.5)$ ). We run 20 simulations for each combination (for a total of 600 runs). For all, reinnovation is socially-mediated ( $S = 1$ ). The results show that various combinations of parameters produces a number of cultural behaviours (pattern  $D$ ) consistent with the 38 found in (3), in absence of any explicit copying mechanism implemented (see Figure 1).

We also analyse the effect of the parameter  $S$  (proportion of socially-mediated reinnovations), in three conditions (see Figure 2): (a) no genetic differences and intermediate ecological differences (compare to the high-left angle of Figure 1,



**Fig. 1.** Number of cultural traits in oranzees, when varying ecological and genetic diversity. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. For all simulations,  $S = 1$ ,  $\alpha_e$  and  $\alpha_{ga} = 0$  as indicated in the plot.  $N = 20$  runs for each parameters combination.

where with  $S = 1$  simulations produce less than 38 cultural behaviours), (b) good match with (3), and (c) intermediate genetic differences and high ecological differences (compare to the low-right angle of Figure 1, where with  $S = 1$  simulations produce more than 38 cultural behaviours). As expected, decreasing  $S$ , decreases the number of cultural behaviours. Conditions where, with  $S = 1$ , there were more than 38 cultural behaviours could still produce results analogous to (3), when not all reinnovations are socially mediated.

Our results show that our model not only easily reproduces the number of cultural behaviours (pattern *D*), but also the number of behaviours classified in the other three patterns (*A*, *B*, *C*) in (3). Figure 3 show the four patterns produced in one of the conditions for which we have a good match for cultural behaviours ( $\alpha_e = 0.8$ ;  $\alpha_g = 0.2$ ,  $S = 1$ ).

Finally, we run 100 simulations for the same condition where we have a good match for cultural behaviours with (3) ( $\alpha_e = 0.8$ ;  $\alpha_g = 0.2$ ,  $S = 1$ ). In each simulation, we recorded, for each population, the number of behaviours (habitual + customary + present) that are also classified as cultural (see Figure 4). We find a small, but significant, correlation between population size and number of cultural traits ( $p < 0.00001$ ,  $\rho = 0.2$ ,  $N = 600$ ). In other words, our model reproduces the effect

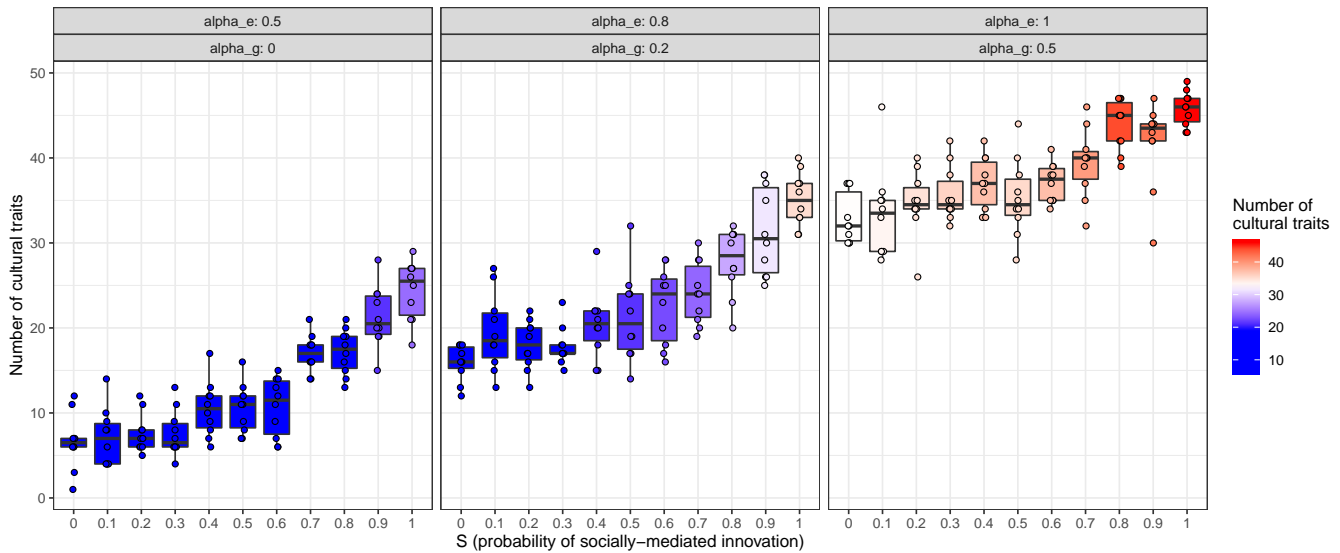
of cultural accumulation relative to population size possibly found in real populations (9, 12, 13).

## Discussion

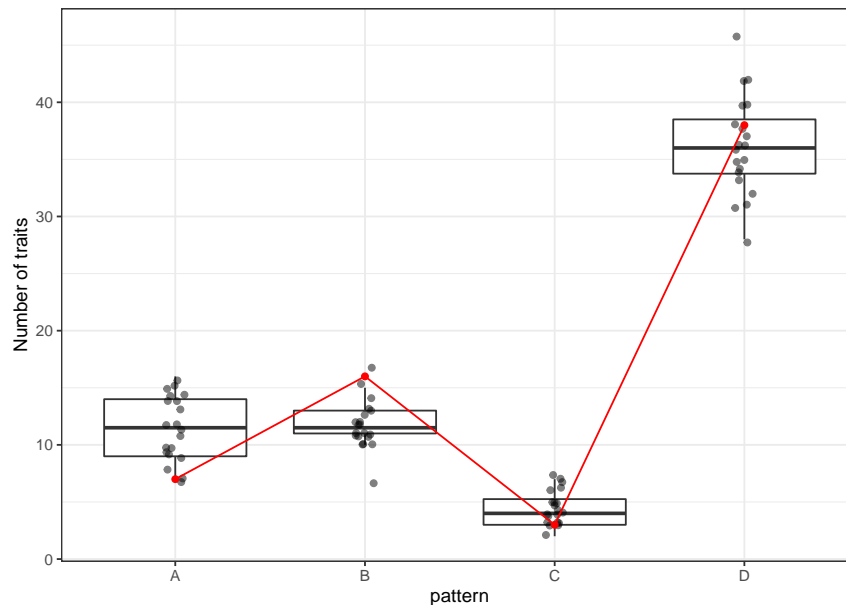
We developed an individual-based model to examine under which conditions a distribution of behavioral traits analogous to the distribution reported in (3) in chimpanzees could emerge, crucially, without the existence of copying mechanisms. We implemented several details of the original study, including realistic demographic and spatial features, as well as effects of genetic propensity and ecological availability on the behaviours.

Our main result is that we can reproduce the same pattern under realistic values of the parameters of genetic propensity and ecological availability, (namely null to medium importance of genetic variation, and medium to high importance of ecological variation.) While we can not precisely pinpoint the exact values that these parameters should have to reproduce real population of chimpanzees, we are confident that the range of values explored, and the relative facility by which patterns of cultural behaviours similar to (3) can be produced in the model, strongly suggest that copying is not required for those patterns to emerge. In addition, and as further support

\*Therefore, ape-like cultural patterns do not and cannot pinpoint copying abilities or necessities.



**Fig. 2.** Cultural traits in oranzees, varying the probability of socially-mediated innovations. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours.  $S$ ,  $\alpha_e$  and  $\alpha_g = 0$  as indicated in the plot.  $N = 10$  runs for each parameters combination. --> Into SI. Instead, add here the "WOW WHITEN FIGURE"



**Fig. 3.** Number of behaviours for each of the four patterns (\*A\*, \*B\*, \*C\*, \*D\*) for the parameters  $\alpha_e = 0.8$ ;  $\alpha_g = 0.2$ ,  $S = 1$ . The red values are the values described for real chimpanzees populations.  $N = 20$  runs.

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to our results, our model not only reproduces the cultural behaviours pattern, but also the proportions among the other patterns, i.e. absent behaviours, behaviours not achieving habitual frequencies at any site, and behaviours absent because of ecological factors.

In our model, we focused on the mechanism of socially mediated reinnovation, that is, we assumed that members of our hypothetical species, oranzees, had a probability to reinnovate a specific behaviour stochastically linked to how many other oranzees in the population were already showing this behaviour. While this is a realistic assumption [REF] and

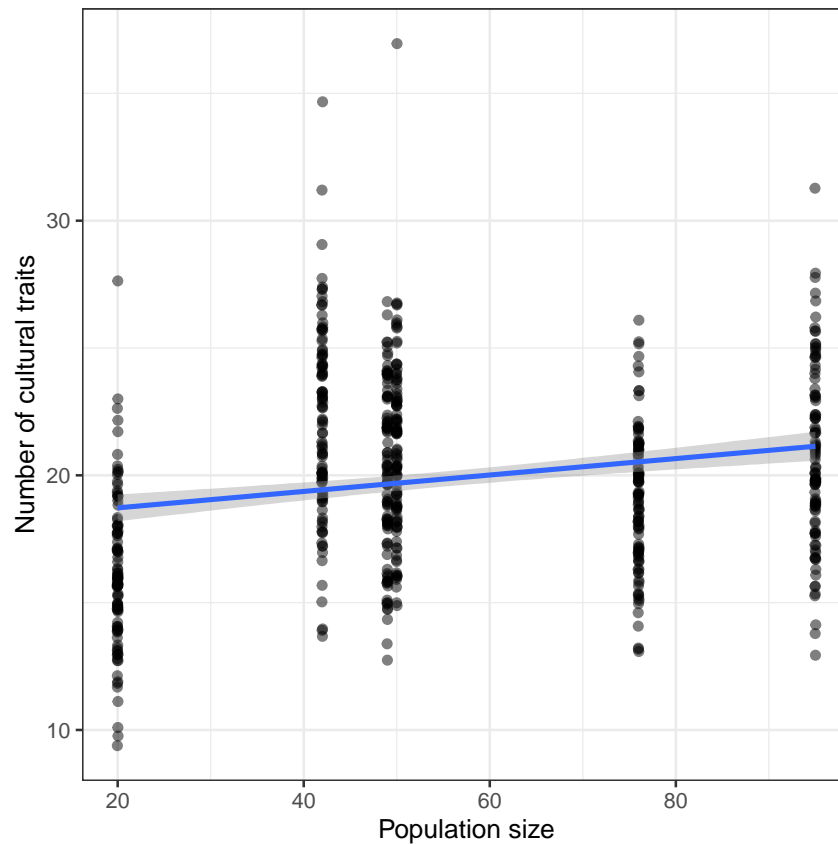
it produces in our model the real chimpanzees cultural pattern observed in realistic conditions, our results show that it is not necessary. Given other combinations of parameters, such as higher genetic and ecological diversities, the cultural pattern can be obtained even when reinnovation is not socially mediated, and oranzees are not influenced by the behaviours of the other individuals. Finally, our model reproduces a correlation between population size and number of cultural traits in the six populations. The magnitude of the effect is small, which is to be expected, given that the presence of this correlation in real populations of apes is currently debated. Again, and importantly, this

\* While this general influence of non-copying social learning mechanisms is covered by the term culture

it has to be noted that this does not make such culture cumulative (again, the latter likely requires copying social learning mechanisms instead).

\*\* compare Tennie et al. 2010 (floating peanut paper)

\*\*\*this sentence would need restructuring



**Fig. 4.** Number of cultural behaviours for each population for the parameters  $\alpha_e = 0.8$ ;  $\alpha_g = 0.2$ ,  $S = 1$ . The blue line is a linear fit of the data.  $N = 100$  runs.

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(as all our results here)

correlation is brought about without copying, so that we do not need to invoke specific “cultural” reasons (e.g. (14)) to explain it: ~~such patterns here or elsewhere.~~

In line with other studies (15, 16), the results of our models suggest caution when deriving individual-level mechanisms from population-level patterns. Cultural systems, as many others, ~~often~~ exhibit equifinality: the same global state can be produced by different local processes. Models and experiments are crucial to test the plausibility of inferences going from

global to local properties. ~~:-) extremely nicely put!!~~

In conclusion, our model strongly suggest that the data available on the behavioural distributions of chimpanzees populations can not demonstrate that chimpanzees possess cultures ~~influenced~~ based on copying. This, in turn, may provide the explanation ~~by~~ of why their cultures are not cumulative.

\*\*\* let alone requiring copying

**ACKNOWLEDGMENTS.** ERC, Mima, etc.

\* potentially this is a shoot in our foot. here we would need to make clear why only we provide for the 1st time a real answer so, need to say here sth like “other models looking at other factors” or so

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