1	Social network architecture and the tempo of cumulative cultural evolution
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26 Abstract

27	The ability to build upon previous knowledge – cumulative cultural evolution (CCE) – is a
28	hallmark of human societies. While CCE depends on the interaction between social systems,
29	cognition and the environment, there is increasing evidence that CCE is facilitated by larger and
30	more structured societies. However, the relative importance of social network architecture as an
31	additional factor shaping CCE remains unclear. By simulating innovation and diffusion of cultural
32	traits in populations with stereotyped social structures, we disentangle the relative contributions
33	of network architecture from those of population size and connectivity. We demonstrate that while
34	multilevel societies can promote the recombination of cultural traits into high-value products, they
35	also hinder spread and make products more likely to go extinct. We find that transmission
36	mechanisms are therefore critical in determining the outcomes of CCE. Our results highlight the
37	complex interaction between population size, structure and transmission mechanisms, with
38	important implications for future research.
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40	Keywords
41	Cultural evolution Cultural complexity Multilevel societies Small-world networks Social
42	structure
43	
44	Introduction
45	
46	Cumulative cultural evolution – where iterative innovations and social transmission generate
47	cultural accumulation over time [1-3] – is key to the human's ecological success and worldwide
48	distribution [4,5]. While CCE fundamentally depends on the interplay between cognition and
49	social learning mechanisms [1], it is increasingly clear that demography can modulate the rate of
50	cultural evolution [6-9]. Large population sizes [10,11], greater population turnover, and more
51	densely connected societies [3,12] can all provide greater innovative potential, more learning
52	models, faster diffusion, and reduced extinction risk of useful innovations [7,13-15]. For example,
53	increasing population density as well as migration of hunter-gatherers during the upper

societies [8,15]. Yet, it remains unclear how variation in the wiring of these social connectionsshape the tempo of cumulative cultural evolution.

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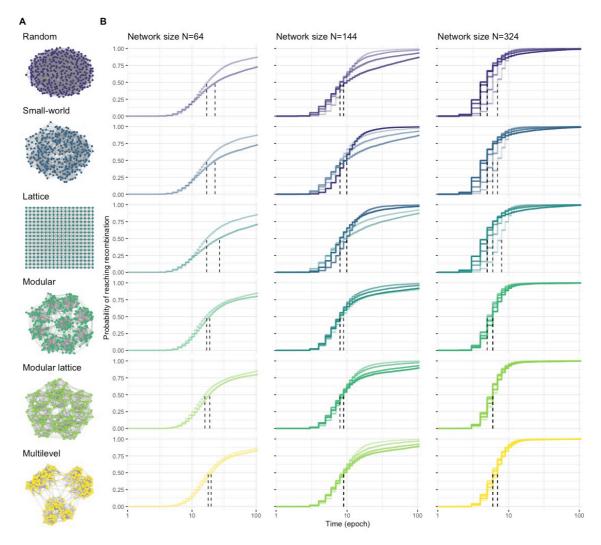
58 Network architecture – here defined as a social structure with a characteristic set of properties – 59 can shape transmission of behaviours, thus setting the tempo of CCE – here defined as the rate of 60 cultural recombination events. For example, architectures with low network connectivity (i.e. 61 density; proportion of realised connections), high clustering (tendency of connected individuals to 62 share the same social neighbours) and high modularity (tendency of the network to contain sets of 63 individuals more connected to each other than with others) slow down the spread of information 64 across populations [16-18]. Slower spread can then potentially favour greater cultural diversity by 65 allowing multiple cultural lineages to arise in populations before any one lineage dominates 66 [19,20]. While previous work has largely focused on how new behaviours spread through a social 67 network [16,17] to establish cultures [20,21] and how cultural traits can generate a feedback shaping network structure [18,22], more recently it has been argued that emergent network 68 69 properties could affect CCE [12,14,19] by shaping how new traits are produced, recombined, and 70 maintained [14]. For example, partial connectivity facilitates the emergence of multiple cultural 71 lineages in parallel [20], which is required for achieving cultural accumulation, but partially-72 connected networks suffer from cultural loss if connectivity is too low for new innovations to 73 spread [14]. By contrast, full connectivity facilitates rapid spread of new innovations, but can 74 prevent the accumulation of alternative cultural traits [12,14]. However, within a given level of 75 connectivity, how connections are structured – the social network architecture – could also impact 76 CCE by influencing how fast and widely information can spread.

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Because network architecture can shape the effect of connectivity on diffusion dynamics [23], those
architectures that balance the ability for cultural accumulation together with the recombination of
different cultural traits should have a selective advantage in facilitating CCE [19]. Multilevel
societies, such as those in modern hunter-gatherers, feature high clustering and nested modularity.
These network properties are expected to favour CCE by allowing coexistence of multiple cultural
traits in different parts of the network, and for different cultural lineages to come into contact to
allow combinations from lineages to produce new traits [19]. Multilevel societies have been

85	demonstrated to accelerate CCE when compared to fully connected networks [19]. However, when
86	considering their potential for facilitating CCE, multilevel and fully-connected networks represent
87	possible endpoints along a continuum of possible architectures. Here, we ask how a range of social
88	network architectures can affect the tempo of CCE within a given population size and number, or
89	density, of social connections within that population. Our approach allows us to explicitly
90	disentangle the relative contribution of network architecture from those of connectivity and
91	population size.
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93	Results
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95	We generated networks with six different architectures – random, small-world, lattice, modular,
96	modular lattice, and multilevel – capturing different levels and combinations of clustering and
97	modularity (Fig. 1A). We expressed these network architectures in populations with different sizes
98	and densities of connections (average degree), where all individuals in the network had the same
99	degree. We then used the agent-based model implemented by Migliano et al. [19] (hereafter model
100	1), inspired by the experiment of Derex & Boyd [12], to explore how network architecture affects
101	time to cultural recombination (i.e. tempo) and the diversity of cultural traits. Briefly, this model
102	allows innovations of cultural products to take place along two cultural lineages, with the
103	knowledge of new products being spread to all social connections (one-to-many diffusion). Once a

- 104 high level of product diversity has been reached in both lineages, agents can recombine each
- 105 lineage's products into one with a final higher payoff product (hereafter 'recombination').
- 106



107

108 Figure 1. Social network architectures, and the time to recombination for each architecture across 109 population sizes and levels of connectivity using model 1. (A) Network architectures vary in 110 clustering and modularity: Random (unclustered C=0.03, non-modular Q=0.24), small-world (clustered 111 C=0.52, medium-modular Q=0.63), lattice (clustered C=0.45, medium-modular Q=0.54), modular

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(unclustered C=0.23, modular Q=0.82), modular lattices (clustered C=0.41, modular Q=0.81), multilevel 113

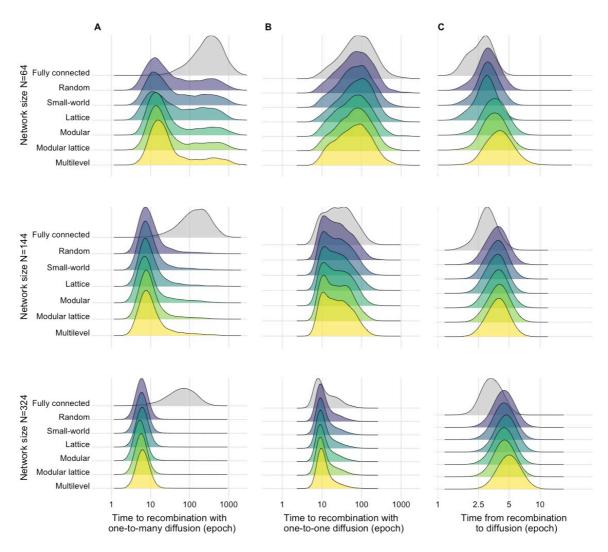
- (clustered C=0.42, modular Q=0.83). Each binary network depicts populations with the same number of 114
- individuals (here, N=324 nodes) that have the same number of social connections (here, degree K=12 115 links per node; density D=0.037) but are wired differently. (B) Cumulative incidence of recombination
- 116 events (y-axis) as a stepwise function over time (x-axis, log epochs) for small (N=64), medium (N=144),
- 117 and large population sizes (N=324). The line shading represents the amount of network connectivity
- 118 (node degree K, where the lighter the shade, the smaller the degree ($K \in \{8,12\}$ for N=64; $K \in \{8,12,18,24\}$
- 119 for N=144; K∈{8,12,18,24,30} for N=324). Vertical dashed lines indicate the median of time to

recombination (S(t) \leq 0.5) per network connectivity, across architectures. The time to reach recombination was truncated to 100 epochs for better visualization. Curves were calculated based on 5,000

122

123 Confirming the effects of population size and connectivity on CCE

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- 125 When comparing time to recombination, we confirm that partially connected networks
- 126 outperform fully connected networks [12,14,19] (Fig. 2A). A generalized linear model indicated
- 127 that overall fully connected networks were, on average, 65% slower (GLM, $\exp(\beta)$ =1.652, t=59.208,
- 128 p<.001; Table S1) compared to the least structured network architecture of the same size (random,
- 129 N=64 taken as the intercept), with similar decreases in performance independent of size. Further,
- 130 we also confirm [7] that larger populations take less time (about 40% less) to reach recombination
- 131 (GLM, $\exp(\beta)=0.618$, t=-68.481, p<.001) compared to networks of the same architecture and
- 132 connectivity (Figs. 1B,2, Table S2). Larger partially-connected network architectures were less
- 133 variable in their time to recombination (Quartile Coefficient of Dispersion: QCD=0.688 for N=64;
- 134 *QCD*=0.444 for N=144; *QCD*=0.273 for N=324, Fig. 2A). We also found that time to recombination
- 135 was optimized at intermediate densities of connections, confirming that intermediate levels of
- 136 connectivity can favour CCE [14], and revealing that the optimal level of connectivity varied with
- 137 population size (Fig. 1B). In the smallest population (N=64), sparse networks outperformed the
- 138 others, but this was reversed in the largest population (N=328) (Fig. 1B). However, differences in
- time to recombination were generally small (Fig. 1B, 2A).
- 140 simulations.





142 Figure 2. Time to recombination and time from recombination to diffusion across network

143 architectures with varying sizes but a fixed degree. Comparison of the performance across the range of 144 network architectures of the same degree (here K=12 link per node) and fully connected networks of the 145 same size (N=64, N=144, and N=324 nodes, K=63, 143, and 323 respectively). (A) Time to recombination 146 (log epochs) from 5,000 simulations with model 1 that uses a broadcast (one-to-many) diffusion 147 dynamic. (B) Time to recombination (log epochs) from 5,000 simulations with model 2 that uses a 148 dyadic (one-to-one) diffusion dynamic. (C) Difference between the time to recombination and the time 149 to diffusion, where time to diffusion corresponds to the latency until the majority of the individuals in 150 the population has information about the final higher-payoff product, from 5,000 simulations using 151 model 2 (one-to-one diffusion). All ridges were plotted with the same bandwidth (0.18). 152

153 Architectures favouring CCE under some conditions disfavour CCE under other conditions

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155 Under the one-to-many diffusion mechanism (model 1), multilevel, modular, and modular lattice 156 architectures had relatively shorter times to recombination in smaller populations with greater 157 connectivity and in larger populations with less connectivity (Fig. 3A). However, such network 158 architectures performed worse than lattice, small world, and random architectures in smaller 159 populations with less connectivity and in larger populations with greater connectivity (Fig. 3A). Multilevel, modular, and modular lattice architectures were optimal at lower and higher levels of 160 161 connectivity in medium-sized populations (N=144, Fig. 3A), although connectivity generally had a 162 lesser impact for these architectures relative to random, small-world, and lattice architectures (Fig. 163 **1B**). Surprisingly, multilevel performed the worst in seven out of the 11 size and connectivity 164 combinations (Fig. 3A) despite having the highest clustering and modularity – properties that 165 have been predicted to favour CCE [19]. The modular lattice architecture (which had similar 166 modularity and clustering to multilevel architecture) performed best in the other four 167 combinations (Fig. 3A). Thus, no one network architecture proved optimal, with those favoured 168 under some conditions being disfavoured under other conditions. 169 170 The large variation in the time to recombination (Fig. 2) within a given combination of network 171 architecture, population size, and density of connections suggests that the outcomes of a simulation were predominantly driven by stochastic events. The impact of such stochasticity is 172 173 best revealed by the bimodal outcome for partially connected networks, which arises most often in 174 smaller populations (Fig. 2A). This bimodality occurs because there are fewer independent 175 innovation events when there are fewer individuals, which increases the chance that cultural 176 products all emerge from the same lineage and, therefore, that this single lineage spreads to the 177 whole population before the other lineage is innovated. Tracking the diversity of products over

178 time (Figs. 4,S1) highlights how the stochasticity in early events can affect cultural diversity, and

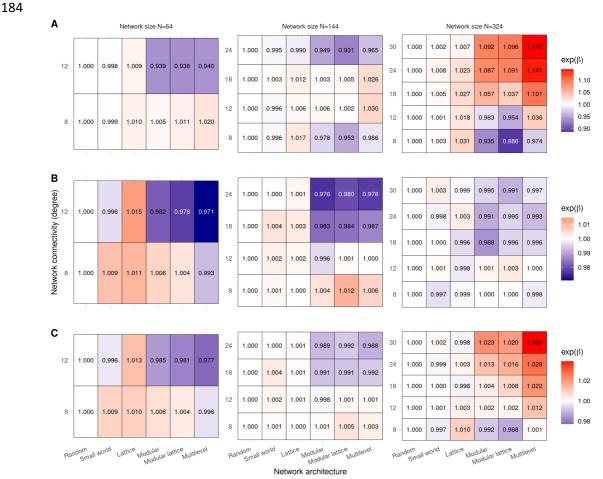
179 therefore the outcomes of CCE, even within the same network architecture. Overall, measuring the

tempo of CCE under one-to-many diffusion (model 1) revealed differences in the best performing

architecture across population sizes and levels of connectivity (Fig. 2A,3A); however, these

between-architecture differences were small (range = 0.886-1.145; Fig. 3A), compared to the large





185 Figure 3. Relative performance of network architectures within each of the 11 combinations of 186 population size and level of connectivity used in the simulations. Each row of each table reports the 187 coefficient estimate of GLMs of network architecture (column) in function of the time to recombination 188 while maintaining degree (row) and network size (box) constant. Red colours (higher coefficients) 189 represent a poorer performance (longer latency to recombination) while blue colours represent 190 architecture that perform better (shorter latency to recombination) for that combination of population 191 size and level of connectivity (using random networks as the reference architecture in the GLM 192 intercept). The relative performance of each architecture is shown for (A) time to recombination under a 193 one-to-many diffusion mechanism (model 1), (B) time to recombination under a one-to-one diffusion 194 mechanism (model 2), and (C) total time to diffusion (from simulation start until the majority of the 195 population has information about the final higher-payoff product) under a one-to-one diffusion 196 mechanism (model 2).

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198 Diffusion mechanisms modify the contribution of network architecture, population size and connectivity on
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- **199** *CCE*
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- 201 To identify the relative contribution of diffusion mechanisms to CCE, we extended model 1 by
- 202 implementing a one-to-one diffusion mechanism (hereafter model 2). Whereas model 1 represents

203 an extreme scenario where information spreads instantaneously to all the contacts of a focal agent, 204 model 2 tests another extreme in which information about discoveries spread only to a single 205 contact at a time. Interestingly, when employing such one-to-one diffusion dynamics, fully 206 connected networks were only estimated to be 3% slower to recombination compared to networks 207 of the same population size (GLM, $\exp(\beta)$ =1.033, t=6.808, p<.001; **Table. S1**). Again, larger 208 populations had a significantly shorter average time to recombination compared to smaller 209 networks of the same architecture and degree (GLM, $\exp(\beta)=0.595$, t=-109.094, p<.001; Fig. 2B, 210 Table. S2). However, under one-to-one diffusion, the relative times to recombination of different 211 architectures was generally more consistent than under one-to-many diffusion, both in their 212 median times to recombination (Fig. 2B) and in their relative performance under a given 213 population size and level of connectivity (Fig. 3B). Within a given population size, multilevel 214 architecture typically had the shortest times to recombination when networks had greater 215 connectivity, but there was almost no difference in performance among architectures when 216 connectivity was low (Fig. 3B). Thus, in contrast to one-to-many, one-to-one diffusion increased 217 the tempo for architectures with greater modularity and clustering (modular, modular lattice, 218 multilevel) relative to the other architectures. 219 220 Model 2 also tracked the time for the recombination product to diffuse to the majority of the 221 population, something which model 1 was not designed to track. The time from recombination to 222 diffusion was shortest in fully connected networks, and increased with population size (Fig. 2C).

223 When evaluating performance from the start of the simulations until the time to diffusion,

224 population size was the main contributor to differences in outcomes (Fig. S5). In small

225 populations, the contribution of the final diffusion was relatively small compared to the time to

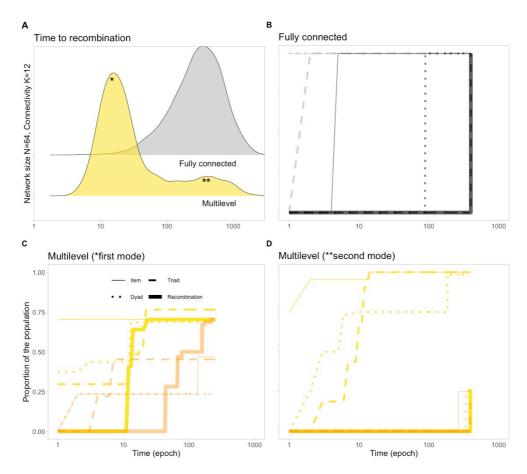
226 recombination, meaning that the best performing networks in achieving recombination also

227 performed best overall (Fig. 3C). By contrast, in larger populations, the performance of modular

and clustered network architectures (modular, modular lattice, and multilevel) all performed

229 worse: they were the slowest at reaching final diffusion (Fig. 3C) despite typically reaching

- 230 recombination the fastest (Fig. 3B). These differences, however, remain minor relative to the
- variance in outcomes within each set of conditions (architecture, population size and connectivity).
- 232



233

234 Figure 4. Cultural product diversity across time in a fully connected network and a highly structured 235 social network architecture illustrates how early stochasticity shapes cultural outcomes. (A) Time to 236 recombination (epochs) from 5,000 simulations with one-to-many diffusion dynamics (model 1) in 237 multilevel and fully-connected networks (with N=64 and K=12). Following panels show cultural 238 diversity over time from one simulation taken from the (B) from the mode of the fully-connected 239 network, and the (C) first (*) and (D) second (**) modes of the distribution of results from the multilevel 240 architecture. Cultural diversity represents the proportion of the population with one of the four possible 241 products over time, from two independent lineages (light and dark shades): a single inventory item (1st 242 stage; thin lines), a combination of two items (2nd stage; dotted lines), a valid combination triad of items 243 (3rd stage; dashed lines), and the final higher payoff product, i.e. a triad recombining products from the 244 two lineages (recombination; thick full lines).

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246 Discussion
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- 248 We revisit recent empirical and *in silico* experiments in humans to tease apart the contributions of
- 249 different candidate social structures to the tempo of cumulative cultural evolution. Our results
- 250 suggest that it is unlikely that one specific social network architecture consistently promotes CCE

across all population sizes, densities of social connections, or diffusion mechanisms. Rather, the
relationship is nuanced; the broad distribution of outcomes from our two models indicate that the
best performing architecture under some conditions can be the worst performing architecture
under others. Further, the outcome of any diffusion mechanism is as likely to be affected by
stochastic processes as by the architecture of the networks itself. While not at odds with previous
work showing that multilevel societies can accelerate CCE [19], our results suggest that a range of
other partially connected architectures could equally increase the tempo of CCE.

258

259 The fact that alternative architectures can have similar outcomes in terms of CCE has important 260 consequences for how the social structure of societies and CCE are framed in future discussions, 261 and where future research is directed. Current thinking is that complex, highly structured 262 societies, such as multilevel societies, might precede recombinatory CCE in the timeline of human 263 evolution, or that the benefits accrued from cultural evolution [22] or CCE [19] might co-evolve 264 with clustered and modular network structures. However, our results suggest that simple patterns 265 of spatial distribution (e.g. a lattice social network caused by distributed resources) could lead to 266 largely equivalent effects on CCE. It follows that we might expect to find recombinatory CCE even 267 before the evolution of complex societies. Indeed, evidence that simple, lattice-like social 268 structures [24] can provide a substrate for recombinatorial culture might be provided by the 269 combinatorial, spatially variable song structure of territorial passerine birds [25-29], which several 270 authors have proposed to be a simple form of CCE [30,31].

271

Population size has been suggested as another major demographic factor affecting rates of CCE 272 273 [3,7-9]. Our findings confirm this previous research, with our simulations showing that larger 274 populations always have a higher rate of cultural accumulation. Population size also interacted 275 with connectivity (which we modelled as a fixed network degree, i.e. the number of individuals' 276 social connections [22]), with changes in connectivity having a more pronounced effect in smaller 277 populations. This outcome is likely to arise because an increase in one unit of mean degree 278 corresponds to a greater increase in network connectivity in smaller populations (more rapidly 279 pushing the network towards becoming fully connected). However, in our simulations we did not 280 vary the distribution in connectivity among individuals, which has previously been shown to

281	impact the properties of information cascades [32] and differences among groups in behaviours
282	such as cooperation [33]. Skewed degree distributions, where some nodes are much more
283	connected than others, could allow independent lineages to arise in peripheral nodes and for
284	highly connected 'hubs' to combine the products from these lineages, thereby facilitating CCE.
285	Thus, variation in how much or how little individuals are connected, independently of other
286	factors (mean connectivity, population size, and network properties), is an important dimension
287	for future studies on CCE to consider.

288

289 Fully connected networks have been commonly used to evaluate the performance of a 290 transmission network with a given set of characteristics [3,19]. Our simulations demonstrate that 291 the contribution of large differences in connectivity outweighs any effects pertaining to 292 architecture, at least when information is broadcast (i.e. a one-to-many diffusion mechanism). 293 Further, for most human societies, a fully-connected social network for a population of any 294 reasonable size would correspond with an unrealistically high level of connectivity [34], even in 295 the higher levels of the fractal-like human social networks [35]. Thus, we suggest that fully 296 connected networks are uninformative null models for testing the influence of social structure on 297 rates of CCE. Instead, random networks of similar sizes and densities of connections as a given 298 network of interest would provide a more robust benchmark for comparing the performance of its 299 architecture. Our results suggest, however, that any effect of network architecture on increased 300 rate of CCE inferred from noisy field data would likely be indistinguishable from the null 301 expectancy, as variation within architecture greatly exceeded that between architectures. 302

303 The evolutionary benefits of CCE not only rely on cultural accumulation, but also on the ability for 304 new cultural traits to spread through populations. When we extended simulations to examine the 305 time from recombination to the diffusion of the final higher payoff product, our results suggested 306 that the network architecture hypothesized to improve time to recombination performance 307 paradoxically inhibited diffusion most. These findings complement and extend the previous study 308 by Derex et al. [12] demonstrating that populations with partially-connected network structures 309 can suffer from cultural loss when connectivity becomes too low for new innovations to spread. 310 Further, the relative performance of architectures can change dramatically when considering

311 performance in terms of acquisition of behaviour by the majority of nodes in a network, as 312 opposed to the time when a single node has reached recombination, especially in larger 313 populations. For example, while multilevel architecture consistently reached recombination faster 314 than random networks under one-to-one diffusion, this architecture then restricted the final 315 spread of higher-value cultural traits. Our results therefore suggest that multiple dimensions of 316 performance – including every step from innovations to the final acquisition of higher-valued 317 traits – may need to be considered when studying the role of social structure in shaping CCE and 318 vice-versa.

319

320 Our work reinforces the need for studies of CCE to explicitly consider how network structure 321 interacts with transmission mechanisms to form a realised transmission network. We show that a 322 very restrictive transmission dynamics (one-to-one) mitigates the effect of network connectivity on 323 CCE by generating a partially connected transmission network within an otherwise fully-324 connected social network. The consequences of transmission dynamics on CCE were 325 demonstrated, for instance, by Migliano et al. [19] who found that CCE was faster in simulations 326 where transmission was limited to kin-based connections (i.e. reduced connectivity). Under one-327 to-one diffusion, independent lineages can develop in fully-connected networks because new 328 information is not immediately accessible to all, leading to more comparable performance between 329 fully and partially connected networks. Thus, when simulating CCE, it is important to match the 330 transmission dynamics with the time scale of the model. One-to-many diffusion can be realistic 331 when each epoch represents one generation (e.g. the innovation of a new medicine [19] could take 332 tens or hundreds of epochs to reach high recombinatory levels), while the one-to-one diffusion 333 might be more realistic when cultural traits are simpler to recombine. The production and 334 innovation frequency, as well as transmission biases, may further vary between species, 335 populations, tasks and contexts. Together with network structure, innovation frequency and 336 transmission biases may fundamentally alter the transmission dynamics – for example, conformity 337 overrides pay-off biases [21,36] and homophily reduces social connectivity [18,37] - fuelling 338 evolutionary feedbacks between network structure and cultural evolution [22]. Both factors will 339 therefore alter the resulting transmission networks, potentially restricting spread of new cultural 340 traits and slowing recombinatory CCE. More than highlighting the intricate, yet nuanced,

- 341 interplay between demography and cultural transmission, our work strengthens our emerging
- 342 understanding that realised connectivity, rather than network architecture, is important for CCE
- 343 [2,3].
- 344
- 345 Materials and Methods
- 346
- 347 Networks
- 348

349 We generated six architectures of binary social networks in which nodes represent individuals 350 linked by social relationships: (i) small-world networks, using the Watts-Strogatz model [23] with 351 node degree K links; (ii) random networks, by randomly connecting nodes ensuring all nodes had 352 the same degree K; (iii) lattices, by placing nodes on a grid and connecting each to its K nearest 353 neighbours; (iv) modular networks, by assigning nodes into nine modules, randomly connecting 354 each to K-1 nodes from the same module and one node from another module; (v) modular lattices, 355 as per modular networks, but where the connections within modules were lattices; and (vi) 356 multilevel networks, as per modular lattices, but assigning nodes into three sets of three modules, 357 and connecting each to K-2 nodes within their module, one node from each module from within its 358 set and one node from a module outside of it. We generated networks with different sizes 359 $(N \in \{64, 144, 324\}$ nodes), and densities of connections (in which $K \in \{8, 12, 18, 24, 30\}$ average links). 360 We used these population sizes because they allowed us to partition the network into equally-361 sized clusters composed of equally-sized groups in which all individuals had the same degree, and 362 in which connectivity was greater within groups and within clusters than between groups and 363 between clusters. 364 365 Network metrics 366 367 Although all networks had comparable sizes and densities (i.e. the proportion links), the six 368 architectures varied in levels and combinations of clustering coefficient and modularity.

369 Clustering, *C*, informs the tendency of connected nodes to share the same connections with other

370 nodes, while modularity, *Q*, informs the tendency of the nodes to be organized into cohesive

371 subsets that are more connected to each other than to the rest of the network [38].

372

373 Simulations

374

375 Our first agent-based model (model 1) followed Migliano et al. [19]. All agents were initialized 376 with an inventory of three items from each of two lineages. In each simulation round (epoch), each 377 focal agent was selected once, at random, and a partner randomly chosen from its social network 378 connections. These agents combined one or two items from their inventory in proportion to their 379 value into a triad of items. If this triad was a valid product, knowledge of that product was 380 learned, spread immediately to all their network connections (one-to-many diffusion), and 381 subsequently became available as an ingredient for making new products. Simulations finished 382 once a recombination product (a triad that recombines specific products from both lineages) was 383 first innovated. We ran 5,000 simulations for each of the network architecture types, sizes and 384 densities of connections, recording time to achieve the recombination product (in epochs) and 385 diversity of innovations in each epoch. An epoch was one simulation round in which each agent 386 was selected once as a focal agent in random order.

387

388 Our second agent-based model (model 2) extended the first by changing the transmission 389 mechanic and altering the set of valid combinations such that the model can run past the first 390 innovation of either recombination product. Transmission of valid products now occurred 391 between dyads of agents (one-to-one diffusion) prior to choosing items from their inventory, in 392 contrast to the broadcast style of diffusion in model 1. Secondly, if a triad contained either 393 recombination products, the final product was that recombination product. In the case where both 394 recombination products were present in the triad, one was chosen as the final product at random. 395 This allowed us to track the diffusion of recombination products beyond their innovation. We also 396 ran 5,000 simulations for the same parameter space of model 1, recording time to recombination 397 and time to diffusion to the majority of the network (in epochs). We implemented the agent-based 398 models in R and Python. The code to generate the social networks, perform the simulations, the 399 statistical analyses and the figures are available at [39]

400

401 Data analyses

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403	To compare the performance of agents organized in different network architectures, we used time-
404	to-event (survival) analyses [40] where time to recombination was a function of architecture and
405	connectivity. For each population size, we used the Cumulative Incidence Function to estimate the
406	proportion of simulations in which agents reached the recombination of each cultural lineage's
407	products into a final high-payoff product. We used the non-parametric Kaplan-Meier product
408	limit estimator to represent the time intervals based on observed recombination events from 5,000
409	simulations from model 1, calculating 95% confidence intervals with the Greenwood estimator. To
410	measure variance in time to recombination across population sizes, we measured the quartile
411	coefficient of dispersion (QCD=(Q3-Q1)/(Q3+Q1)), as this variable is not normally distributed and
412	QCD offers a more robust measure.

413

414 While statistics are not typically performed on data from agent-based models since the posterior is 415 directly sampled, we wanted to quantify the relative contributions of architecture, size and 416 connectivity without the cumbersome descriptions of the entire distribution (which can be readily 417 seen in Fig. 2). For both models 1 and 2, we created three sets of generalized linear models (GLMs) 418 that predicted logged time to recombination (in epochs). Time to recombination was logged to 419 account for non-normality of residuals, and to make comparisons more fair by bringing the mean 420 closer to the median of the distribution. All models used log link function, as the data was non-421 linear conditional on predictors, even after the log transformation. Also, the log link function 422 allowed the presentation of exponentiated coefficients, which simplify the comparison to the 423 reference (here, the random networks at the GLM intercept). The first set of GLMs used a full 424 interaction structure to partition the relative contributions of architecture, size and connectivity to 425 average time to recombination (Table S1), excluding fully connected networks. To then compare 426 fully connected networks to all other networks, we built a GLM using architecture and population 427 size as predictors in a full interaction structure (Table S2). Connectivity was excluded as a 428 predictor, as all fully connected networks only have 1 possible degree (K=N-1). Finally, to compare 429 differences between architectures in Fig. 3 more precisely, we subset data by connectivity and

430	population size and performed a GLM with only architecture as a predictor for each subset, again
431	excluding fully connected networks. We performed all data analyses in R [41], using 'survival' [42]
432	and 'survminer' [43] packages.
433	
434	Competing interests
435	
436	The authors have no competing interests with this study
437	
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439	
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450	
451	References
452	
453	1. M. Tomasello, The human adaptation for culture. Annual Rev. Anthrop. 28(1), 509-529 (1999).
454	2. A. Mesoudi, A. Thornton, What is cumulative cultural evolution? Proc. R. Soc. B. 285(1880),
455	20180712 (2018).
456	3. M. Derex, A. Mesoudi, Cumulative cultural evolution within evolving population structures.
457	Trends Cogn. Sci. (In press).
458	4. R. Boyd, P.J. Richerson, The origin and evolution of cultures. Oxford University Press, Oxford
459	(2005).

- 460 5. R. Boyd, P.J. Richerson, J. Henrich, The cultural niche: Why social learning is essential for
- 461 human adaptation. *Proc. Natl. Acad. Sci.* **108**, 10918–10925 (2011).
- 462 6. S. Shennan, Demography and cultural innovation: a model and its implications for the
- 463 emergence of modern human culture. *Cambridge Arch. J.* **11(1)**:5-16 (2001).
- 464 7. J. Henrich, Demography and cultural evolution: How adaptive cultural processes can produce
- 465 maladaptive losses the Tasmanian case. Am. Antiq. 69(2), 197–214 (2004).
- 466 8. A. Powell, S. Shennan, M.G. Thomas, Late Pleistocene demography and the appearance of
- 467 modern human behavior. *Science* **324(5932)**, 1298–1301 (2009).
- 468 9. M. Derex, M.-P. Beugin, B. Godelle, M. Raymond, Experimental evidence for the influence of

469 group size on cultural complexity. *Nature* **503(7476)**, 389–391 (2013).

- 470 10. N. Fay, N. de Kleine, B. Walker, C.A. Caldwell, Increasing population size can inhibit
- 471 cumulative cultural evolution. Proc. Natl. Acad. Sci. 116(14), 6726-6731 (2019).
- 472 11. J. P. Martens, Scenarios where increased population size can enhance cumulative cultural
- 473 evolution are likely common. *Proc. Natl. Acad. Sci.* **116(35)**, 17160-17160 (2019).
- 474 12. M. Derex, R. Boyd, Partial connectivity increases cultural accumulation within groups. *Proc.*
- 475 Natl. Acad. Sci. 113(11), 2982-2987 (2016).
- 476 13. R. Baldini, Revisiting the effect of population size on cumulative cultural evolution. J. Cogn.
- 477 *Cult.* **15(3-4)**, 320-336 (2015).
- 478 14. M. Derex, C. Perreault, R. Boyd, Divide and conquer: intermediate levels of population
- 479 fragmentation maximize cultural accumulation. *Phil. Trans. R. Soc. B* 373(1743), 20170062 (2018).
- 480 15. J. Henrich, R. Boyd, M. Derex, M.A Kline, A. Mesoudi, M. Muthukrishna, A.T. Powell, S.J.
- 481 Shennan, M.G. Thomas, Understanding cumulative cultural evolution. *Proc. Natl. Acad. Sci.*
- **482 113(44)**, E6724-E6725 (2016).
- 483 16. B. Voelkl, R. Nöe, The influence of social structure on the propagation of social information in
- 484 artificial primate groups: a graph-based simulation approach. J. Theor. Biol. 252(1), 77-86 (2008)
- 485 17. C.L. Nunn, P.H. Thrall, K. Bartz, T. Dasgupta, C. Boesch, Do transmission mechanisms or social
- 486 systems drive cultural dynamics in socially structured populations? *An. Behav.* 77(6),1515-1524
 487 (2009).
- 488 18. M. Cantor, H. Whitehead, The interplay between social networks and culture: theoretically and
 489 among whales and dolphins. *Phil. Trans. R. Soc. B* 368(1618), 20120340 (2013).

- 490 19. A.B. Migliano, F. Battiston, S. Viguier, A.E. Page, M. Dyble, R. Schlaepfer, D. Smith, L. Astete,
- 491 M. Ngales, J. Gomez-Gardenes, V. Latora, Hunter-gatherer multilevel sociality accelerates
- 492 cumulative cultural evolution. *Science Adv.* **6**(9), p.eaax5913 (2020).
- 493 20. H. Whitehead, D. Lusseau, Animal social networks as substrate for cultural behavioural
- 494 diversity. J. Theor. Biol. 294,19-28 (2012).
- 495 21. L.M. Aplin, D.R. Farine, J. Morand-Ferron, A. Cockburn, A. Thornton, B.C. Sheldon,
- **496** Experimentally induced innovations lead to persistent culture via conformity in wild birds.
- 497 *Nature* 518(7540), 538-541 (2015).
- 498 22. M., Smolla, E. Akçay, Cultural selection shapes network structure. *Sci. Adv.* 5(8), eaaw0609
 499 (2019).
- 500 23. D.J. Watts, S.H. Strogatz, Collective dynamics of 'small-world' networks. *Nature* 393(6684), 440501 442 (1998)
- 502 24. J.A. Firth, B.C. Sheldon, Social carry-over effects underpin trans-seasonally linked structure in a
 503 wild bird population. *Ecol. Lett.* 19(11), 1324-1332 (2016).
- 504 25. J.P. Hailman, M.S. Ficken. Combinatorial animal communication with computable syntax:
- 505 chick-a-dee calling qualifies as 'language' by structural linguistics. *An. Behav* 34, 1899–1901
 506 (1986).
- 507 26. L.L. Bloomfield, I. Charrier, C.B. Sturdy, Note types and coding in parid vocalizations. II: The

508 chick-a-dee call of the Mountain Chickadee (*Poecile gambeli*). *Can. J. Zool.* 82, 780–793 (2004).

- **509** 27. D.E. Kroodsma, Winter Wren singing behavior: a pinnacle of song complexity. *Condor* **82**, 357–
- **510** 365 (1980).
- 511 28. D.W. Leger, First Documentation of combinatorial song syntax in a suboscine passerine
 512 species. *Condor* 107(4), 765–774 (2005).
- 513 29. C.L. Branch, V.V. Pravosudov, Mountain chickadees from different elevations sing different
- songs: acoustic adaptation, temporal drift or signal of local adaptation?. *R. Soc. Open Sci* 2.4,
 150019 (2015).
- 516 30. L. M. Aplin, Culture and cultural evolution in birds: a review of the evidence. *Anim. Behav.* 147,
 517 179-187 (2019).
- 518 31. A. Whiten, Cultural evolution in animals. Ann. Rev. Ecol. Evol. System. 50, 27-48 (2019).

519 32. D.J. Watts, A simple model of global cascades on random networks. Proc. Natl. Acad. Sci. 99(9),

520 5766-5771 (2002).

- **521** 33. C.L. Apicella, F.W. Marlowe, J.H. Fowler, N.A. Christakis, Social networks and cooperation in
- 522 hunter-gatherers. *Nature* **481(7382)**, 497-501 (2012).
- 523 34. B.J. West, G.F. Massari, G. Culbreth, R. Failla, M. Bologna, R.I.M. Dunbar, P. Grigolini, Relating
- size and functionality in human social networks through complexity. *Proc. Natl. Acad. Sci.*
- **525 117(31)**, 18355-18358 (2020).
- 526 35. R.I.M. Dunbar, Structure and function in human and primate social networks: implications for
- 527 diffusion, network stability and health. *Proc. R. Soc. A* 476:20200446 (2020).
- 528 36. K.K. Denton, Y. Ram, U. Liberman, M.W. Feldman, Cultural evolution of conformity and
- 529 anticonformity. Proc. Natl. Acad. Sci. (In press).
- 530 37. M. McPherson, L. Smith-Lovin, J.M. Cook, Birds of a feather: Homophily in social networks.
- 531 *Annual Review of Sociology*, 27(1), 415-444 (2001).
- 532 38. M. Newman, *Networks*. Oxford University Press (2018).
- 533 39. M. Cantor, M. Chimento, S.Q. Smeele, P. He, D. Papageorgiou, L.M. Aplin, D.R. Farine. 2020.
- 534 Social network architecture and the tempo of cumulative cultural evolution. Github repository.
- 535 <u>https://github.com/simeonqs/Social_network_architecture_and_the_tempo_of_cumulative_c</u>
- 536 <u>ultural_evolution</u>
- 40. R.G. Miller Jr, Survival analysis (Vol. 66). John Wiley & Sons (2011).
- 538 41. R Core Team. R: A language and environment for statistical computing. R Foundation for
- 539 Statistical Computing, Vienna, Austria. URL <u>https://www.R-project.org/</u> (2019).
- 540 42. T. Therneau, A Package for Survival Analysis in R. R package version 3.2-3, <u>https://CRAN.R-</u>
- 541 project.org/package=survival (2020)
- 542 43. A. Kassambara, M. Kosinski, P. Biecek, Survminer: Drawing Survival Curves using 'ggplot2'. R
- 543 package version 0.4.7. <u>https://CRAN.R-project.org/package=survminer</u> (2020)

544 Supporting Material for:

545 Social network architecture and the tempo of cumulative cultural evolution

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554

Table S1. Generalized linear models (GLMs) for agent-based model 1 (with one-to-many
diffusion mechanism) and model 2 (one-to-one diffusion), in which time to recombination
(time to recombination, measured as log(epoch+1)) is predicted by an interaction between

(time to recombination, measured as tog(epocn+1)) is predicted by an interaction between

558 population size and architecture. Coefficients and standard errors are exponentiated, as these

559 GLMs used a log link function. Connectivity was not included, as this contains the same

560 information as population size for fully connected networks. Intercepts represents random

- 561 networks of population size N=64. (*p<0.1; **p<0.05; ***p<0.01)
- 562

	model1		mod	model2		
	p-			p-		
	Estimate	value	Estimate	value		
Constant	3.425***	-0.003	4.205***	-0.002		
graphsmall_world	0.999***	-0.004	1.003***	-0.002		
graphlattice	1.010***	-0.004	1.013***	-0.002		
graphmodular	0.970***	-0.004	0.994***	-0.002		
graphmodular_lattice	0.972***	-0.004	0.991***	-0.002		
graphmultilevel	0.977***	-0.004	0.982***	-0.002		
graphfull	1.652***	-0.003	1.033***	-0.003		
pop_size144	0.715***	-0.004	0.759***	-0.002		
pop_size324	0.512***	-0.004	0.587***	-0.003		
graphsmall_world:pop_size144	0.999***	-0.005	0.999***	-0.003		
graphlattice:pop_size144	0.996***	-0.005	0.989***	-0.003		
graphmodular:pop_size144	1.013***	-0.005	0.996***	-0.003		
graphmodular_lattice:pop_size144	0.999***	-0.005	1.003***	-0.003		
graphmultilevel:pop_size144	1.024***	-0.005	1.011***	-0.003		
graphfull:pop_size144	1.206***	-0.005	0.994***	-0.005		
graphsmall_world:pop_size324	1.005***	-0.006	0.997***	-0.004		
graphlattice:pop_size324	1.012***	-0.006	0.986***	-0.004		
graphmodular:pop_size324	1.059***	-0.006	1.001***	-0.004		
graphmodular_lattice:pop_size324	1.036***	-0.006	1.006***	-0.004		
graphmultilevel:pop_size324	1.100***	-0.006	1.015***	-0.004		
graphfull:pop_size324	1.406***	-0.006	0.980***	-0.005		
Observations	345,0	000	345,	000		
Log Likelihood	-446,7	18.40	-378,0	-378,097.40		
Akaike Information Criterion	893,47	893,478.70		756,236.80		

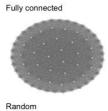
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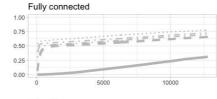
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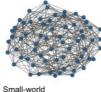
- 564 Table S2. Generalized linear models (GLMs) for agent-based model 1 (with one-to-many
- 565 diffusion mechanism) and model 2 (one-to-one diffusion), in which time to recombination
- 566 (time to recombination, measured as log(epoch+1)) is predicted by an interaction between
- 567 population size, network architecture, and connectivity (i.e. average network degree).
- 568 Coefficients and standard errors are exponentiated, as these GLMs used a log link function.
- 569 Full networks were excluded. Intercepts represent random networks of population size *N*=64,
- 570 average degree of *K*=8. (*p<0.1; **p<0.05; ***p<0.01)
- 571

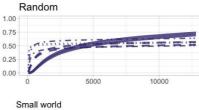
	moo	del1	model2		
	Estimate	p-value	Estimate	p-value	
Constant	3.196***	-0.004	4.168***	-0.002	
graphsmall_world	0.999***	-0.005	1.009***	-0.003	
graphlattice	1.010***	-0.005	1.011***	-0.003	
graphmodular	1.005***	-0.005	1.006***	-0.003	
graphmodular_lattice	1.011***	-0.005	1.004***	-0.003	
graphmultilevel	1.020***	-0.005	0.993***	-0.003	
pop_size144	0.724***	-0.007	0.756***	-0.004	
pop_size324	0.618***	-0.007	0.595***	-0.005	
degree12	1.143***	-0.005	1.018***	-0.003	
degree18	0.847***	-0.01	0.996***	-0.006	
degree24	0.831***	-0.01	0.995***	-0.006	
degree30	0.856***	-0.01	0.992***	-0.006	
graphsmall_world:pop_size144	0.997***	-0.009	0.992***	-0.006	
graphlattice:pop_size144	1.007***	-0.009	0.989***	-0.006	
graphmodular:pop_size144	0.973***	-0.009	0.998***	-0.006	
graphmodular_lattice:pop_size144	0.942***	-0.009	1.008***	-0.006	
graphmultilevel:pop_size144	0.967***	-0.009	1.014***	-0.006	
graphsmall_world:pop_size324	1.004***	-0.01	0.987***	-0.007	
graphlattice:pop_size324	1.021***	-0.01	0.988***	-0.007	
graphmodular:pop_size324	0.930***	-0.011	0.993***	-0.007	
graphmodular_lattice:pop_size324	0.876***	-0.011	0.996***	-0.007	
graphmultilevel:pop_size324	0.955***	-0.01	1.005***	-0.007	
graphsmall_world:degree12	0.999***	-0.007	0.987***	-0.005	
graphlattice:degree12	1.000***	-0.007	1.004***	-0.005	
graphmodular:degree12	0.934***	-0.007	0.976***	-0.005	
graphmodular_lattice:degree12	0.928***	-0.007	0.974***	-0.005	
graphmultilevel:degree12	0.922***	-0.007	0.978***	-0.005	
graphsmall_world:degree18	1.002***	-0.014	1.003***	-0.008	
graphlattice:degree18	0.996***	-0.013	0.997***	-0.008	
graphmodular:degree18	1.131***	-0.014	0.988*** 0.996***	-0.008	
graphmodular_lattice:degree18	1.170*** 1.130***	-0.014	0.996***	-0.008 -0.008	
graphmultilevel:degree18	1.005***	-0.013 -0.014	1.002***	-0.008	
graphsmall_world:degree24	0.992***	-0.014	1.002		
graphlattice:degree24	1.163***	-0.014 -0.014	0.991***	-0.008 -0.008	
graphmodular:degree24 graphmodular_lattice:degree24	1.231***	-0.014	0.991 0.996***	-0.008	
0 1 0	1.172***	-0.014	0.996	-0.008	
graphmultilevel:degree24 graphsmall_world:degree30	0.999***	-0.013	1.006***	-0.008	
graphlattice:degree30	0.999	-0.014	1.000***	-0.008	
graphmodular:degree30	1.168***	-0.013	0.996***	-0.008	
graphmodular_lattice:degree30	1.237***	-0.013	0.990	-0.008	
graphmultilevel:degree30	1.175***	-0.014	0.992	-0.008	
pop_size144:degree12	0.864***	-0.009	0.999	-0.008	
pop_size324:degree12	0.796***	-0.011	0.975***	-0.007	
pop_size144:degree18	1.251***	-0.011	1.023***	-0.007	
pop_size144:degree24	1.426***	-0.012	1.020	-0.007	
	1.000***	-0.012	1.014***	-0.007	
graphsmall_world:pop_size144:degree12 graphlattice:pop_size144:degree12	0.989***	-0.013	0.998***	-0.008	
graphmodular:pop_size144:degree12	1.101***	-0.013	0.998 1.017***	-0.008	
graphmodular_lattice:pop_size144:degree12 graphmodular_lattice:pop_size144:degree12	1.134***	-0.013	1.017***	-0.008	
graphmultilevel:pop_size144:degree12	1.134	-0.013	1.016***	-0.008	
graphsmall_world:pop_size324:degree12	0.999***	-0.015	1.010	-0.003	
graphlattice:pop_size324:degree12	0.999	-0.015	0.995***	-0.01	
graphmodular:pop_size324:degree12	1.125***	-0.015	1.027***	-0.01	
graphmodular_lattice:pop_size324:degree12	1.125	-0.015	1.027	-0.01	
graphmultilevel:pop_size324:degree12	1.154***	-0.018	1.024***	-0.01	
graphsmall_world:pop_size1244:degree18	1.005***	-0.015	1.024	-0.01	
Supromun_wond.pop_sizer+.ucgreeto	1.000	-0.017	1.000	-0.01	

graphlattice:pop_size144:degree18	0.999***	-0.017	1.006***	-0.01
graphmodular:pop_size144:degree18	0.907***	-0.017	0.991***	-0.01
graphmodular_lattice:pop_size144:degree18	0.902***	-0.017	0.977***	-0.01
graphmultilevel:pop_size144:degree18	0.921***	-0.017	0.982***	-0.01
graphsmall_world:pop_size144:degree24	0.994***	-0.017	0.997***	-0.01
graphlattice:pop_size144:degree24	0.981***	-0.017	0.998***	-0.01
graphmodular:pop_size144:degree24	0.835***	-0.017	0.981***	-0.01
graphmodular_lattice:pop_size144:degree24	0.794***	-0.017	0.973***	-0.01
graphmultilevel:pop_size144:degree24	0.836***	-0.017	0.977***	-0.01
Observations	330,000		330,000	
Log Likelihood	-423,477.80		-359,565.20	
Akaike Information Criterion	aike Information Criterion 847,087.60		719,262.30	









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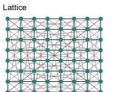
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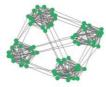
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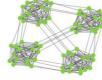


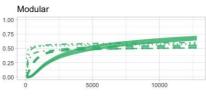


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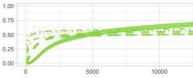




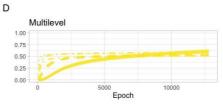




Modular lattice



Multilevel



574 Figure S1. Cultural trait diversity across social network architectures and proposed null

575 **models.** Comparison of the diversity of cultural traits along the network architecture

576 spectrum, across populations of same size (*N*=64 nodes) and connectivity (average degree

577 *K*=12 links) in relative to a fully connected network of the same size (*N*=64, *K*=63). Cultural

578 innovation diversity across network architectures measured as the proportion of the

579 population with one of the four possible traits over time: a single inventory item (dotted

580 lines), a single combination of two items (dashed and dotted lines), a valid combination of

581 three items (triad; dashed lines), and a recombination product (a triad that recombines

582 specific products from both lineages; thick lines). The inventory items came from two

583 independent lineages, represented by lines of the same type.