Animal social networks as substrate for cultural behavioural diversity

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ABSTRACT

We used individual-based stochastic models to examine how social structure influences the diversity of socially learned behaviour within a non-human population. For continuous behavioural variables we modelled three forms of dyadic social learning, averaging the behavioural value of the two individuals, random transfer of information from one individual to the other, and directional transfer from the individual with highest behavioural value to the other. Learning had potential error. We also examined the transfer of categorical behaviour between individuals with random directionality and two forms of error, the adoption of a randomly chosen existing behavioural category or the innovation of a new type of behaviour. In populations without social structuring the diversity of culturally transmitted behaviour increased with learning error and population size. When the populations were structured socially either by making individuals members of permanent social units or by giving them overlapping ranges, behavioural diversity increased with network modularity under all scenarios, although the proportional increase varied considerably between continuous and categorical behaviour, with transmission mechanism, and population size. Although functions of the form $e^{c_1 m^{-c_2} + c_3 Log(N)}$ predicted the mean increase in diversity with modularity (m) and population size (N), behavioural diversity could be highly unpredictable both between simulations with the same set of parameters, and within runs. Errors in social learning and social structuring generally promote behavioural diversity. Consequently, social learning may be considered to produce culture in populations whose social structure is sufficiently modular.

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0. Introduction

Culture is transmitted by social learning (Cavalli-Sforza and Feldman, 1981; Laland and Hoppitt, 2003), and so cultural information transmits over social networks. Thus social structure has the potential to affect, strongly, the forms of social learning and culture shown by a population (Coussi-Korbel and Fragaszy, 1995), as well as to shape the consequences of this culture for population biology and ecology (Flack et al., 2006). For instance, Rendell and Whitehead (2001) have suggested that the matrilineal social structures characteristic of the larger odontocete whales (such as the killer whales, *Orcinus orca,* and sperm whales, *Physeter macrocephalus*) tend to produce stable vertically (between-generation) transmitted group-specific cultures, whereas the more labile social relationships of the baleen whales (suborder Mysticeti) lead to transient horizontally (within-generation) transmitted cultural forms, which can vary with time consistently over large spatial areas. Thus social structure has the potential to affect the emergence of cultural behaviour, its persistence, and its diversity.

Previous work has shown that network structure influences the manner in which processes (e.g., disease, information, opinion, culture) propagate within social systems. Three propagation characteristics are influenced by network topology. First, the number of individuals in the network reached by the process can depend on the network's degree frequency distribution; that is the frequency distribution of the number of connections that individuals possess (Meyers et al., 2005). Second, the rate at which an equilibrium state is reached (when it exists) depends on the modularity of the network. For example, individuals will reach opinion consensus faster in random networks than in hierarchically connected networks, so that the time it takes for an opinion to predominate the network will depend on its modularity (Li and Hui, 2008; Nardini et al., 2008; Voelkl and Noë, 2010). Finally, the equilibrium diversity of the dynamic process (e.g., the number of opinions present on the networks, or the cultural diversity of a population) depends on the mechanisms through which the process propagates and the likelihood that individuals with the same values (same opinion) will cluster (Holme and Newman, 2006).

Diversity is a particularly important characteristic of any system, and particularly any living system. Phenotypic diversity is a prerequisite for evolution through natural selection. The amount of diversity governs the evolutionary potential of the system. Phenotypic diversity is also a large factor in the ecological role that a species assumes (Post and Palkovacs, 2009).

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Preserving diversity, at all levels, is a fundamental goal of conservation biology. For all these reasons, there has been much work, both theoretically and empirically, on genetic diversity. But in some organisms phenotypic diversity is a function of both genes and culture. Human cultural diversity has been a major focus of research in several disciplines with many theoretical studies (e.g. Holme and Newman, 2006; Nakamaru and Levin, 2004) complementing the vast amount of empirical data collected by anthropologists and others. Outside *Homo sapiens* research on cultural diversity is sparse. It has been charted in a very few field studies (e.g. van Schaik et al., 2003), and received little theoretical attention. Most theoretical studies that consider how human cultural diversity may depend upon network structure are not directly applicable as they use binary rather than weighted networks (see Lusseau et al., 2008 for why weighted networks are suitable for non-human social systems), and consider much larger social structures than are general in non-human cultural species. The small social networks with weighted edges arranged non-randomly that are characteristic of non-human societies largely rule out analytical approaches to the question of how network structure affects culturally transmitted phenotypic diversity.

Instead we can address the influence of network structure on cultural evolution by simulating cultural transmission over networks with known structural parameters. Voelkl and Noë (2008) and Nunn et al. (2009) modelled the spread of cultural innovations over different forms of primate social network using individual-based stochastic models. In order to examine diversity directly, we modify these approaches by considering the heterogeneity of quantitative and qualitative cultural traits in social networks of different forms, calibrated to mimic those of non-human species for whom culture is potentially important.

The extent, nature, and even existence of culture in non-humans are all contentious (Laland and Galef, 2009). However, there is strong evidence that social learning does occur in a wide range of species (Galef and Laland, 2005) and we know that network structure can influence the stability and predominance of traits propagating on social networks (Newman, 2003; Nunn et al., 2009). Therefore, there is strong support for investigating how cultural traits transmit and vary over animal social networks as the emergent products of social learning processes on given social network structures, and there have been a few explorations of this. Voelkl and Noë (2010, 2008) explored the propagation of information through simulated and real (in the sense of constructing social networks using data collected from real groups) primate social groups, finding that social structure influenced the speed with which information moves through the society, as well as the proportion of individuals possessing the information. Nunn et al. (2009) studied the dynamics of innovations within socially structured populations. They found that compared to some demographic and social factors, features of the transmission process, such as prestige and consensus transmission, had generally weaker effects. In these analyses, the incidence of a particular trait, or pair of traits was tracked as it transmitted through a social structure. Here we go a step further, looking at the diversity of behaviour being propagated over non-human networks.

In general social structuring would be expected to increase the diversity of culturally transmitted behaviour (Wrangham et al., 1994), But by how much? And how might this depend on the form of social structure, on the type of information, the manner in which information is transferred and on the size of the population? How consistent is this increase in diversity with the degree of social structuring, and how well can it be predicted? These are the questions we examine.

1. Methods

The simulations model the flow of quantitative and qualitative information through a social network, a weighted rather than binary

Table 1
Variables and parameters.

a_{ij}	Association index between individuals i and j
d	SD of δ
g	Number of units in unit-based social system
h'	Shannon's information index
m	Modularity (Newman, 2004)
N	Population size in the simulations
p_k	Proportion of individuals with behaviour category k
q	Number of categorical cultural behavioural values in the population's repertoire
r_{ij}	Distance between range centroids of individuals i and j in spatially based social system
t	Time steps
$x_{i,t}$	Cultural behavioural value of individual i at time step t
β	Parameter indicating ranging behaviour of individuals in spatially based social systems
$\delta_{i,t}$	Learning error of individual i at time t (normally distributed around 0)
μ	Rate of interaction among members of different social units in unit-based social system

(1:0) network, as weighted networks are generally better representations of animal social systems (Lusseau et al., 2008). As in Voelkl and Noë (2008), the network is defined by a temporally invariant symmetric matrix of association indices ($\{a_{ij}\}$, where a_{ij} is the association index between individuals i and j, Table 1) whose entries are proportional to the amount of time that each dyad spends associated (Cairns and Schwager, 1987; Whitehead and Dufault, 1999), and so are assumed to be in a position to transmit information to one another. Individuals encounter one another sequentially and exchange information. Individual i has a cultural behavioural value $x_{i,t}$ at encounter (time step) t. We are interested in the distribution of $\{x_{i,t}\}$, and especially their diversity, as they change through time. In our simulations we used the number of encounters as a metric of temporal progression, but it will be related to real time by a parameter proportional to the sum of association indices in the population. Thus, in larger populations encounters generally occur more frequently than in smaller ones, and a few highly connected individuals in a population will increase the rate of encounters per unit time compared with an otherwise identical population in which these individuals had modal connectivity. The rates of association per unit time of any pair of individuals are unaffected by the population size or the presence of other animals that are particularly well connected in the population.

There are two versions of the model: continuous behaviour in which $\{x_{i,t}\}$ are real numbers, and categorical behaviour in which the $\{x_{i,t}\}$ can take on any of q states. An example of continuous behaviour might be the time spent in some social interaction, or the pitch of a vocalisation. Categorical behaviour would include distinct methods of processing a food type, and places to cross a stream.

At each encounter, t, the routine chooses one dyad among all the dyads with probability proportional to their association, so that the probability that i and j are chosen is: $a_{ij}/\Sigma a_{ij}$. The two members of the chosen dyad then exchange information, to make $x_{i,t+1}$ and $x_{j,t+1}$ ($x_{k,t+1}=x_{k,t}$ if k is not a member of the chosen dyad). We examined three exchange mechanisms, averaging, random donor, and directional transfer, which operated rather differently for continuous and categorical behaviour.

1.1. Continuous behaviour

In this form of the model the initial behavioural value for each individual, $\{x_{i1}\}$, was randomly chosen from the uniform distribution on the interval [0,1].

The three methods of transferring information about continuous behaviour were:

Averaging : $x_{i,t+1} = (x_{i,t}+x_{j,t})/2 + \delta_{i,t}; x_{j,t+1} = (x_{i,t}+x_{j,t})/2 + \delta_{j,t}$

(If two animals with different frequency pitches of the greeting vocalisation meet, they both subsequently use roughly the mean of their frequencies.)

Random transfer : $x_{i,t+1} = x_{j,t} + \delta_{i,t}; x_{j,t+1} = x_{j,t}$

{donor, j, selected randomly from dyad}

(Here, one animal adopts approximately the frequency pitch of the other.)

Directional transfer : $x_{i,t+1} = x_{j,t} + \delta_{i,t}; x_{j,t+1} = x_{j,t}${donor, j, has $x_{j,t} > x_{i,t}$}

(Here the animal with the lower pitched call adopts approximately the frequency of the higher call.)

In these formulations, δ is the learning error, normally distributed with mean 0 and standard deviation (SD) d.

With continuous behaviour we measured behavioural diversity at time t by $SD(x_{i,t})$.

1.2. Categorical behaviour

In this form of the model the initial behavioural value for each individual, $\{x_{i1}\}$, was randomly chosen from q categories, with equal probability for each category.

We only present results from a categorical analogue of the random method of information transfer, so that one of the interactants subsequently adopts the behaviour of the other. Analogues of the averaging and directional methods, in which the categories were ranked, produced quite trivial results with rapid convergence to the mean or maximal categories respectively, and no diversity.[1] At each encounter, categorical information was transferred between individuals i and j as follows:

With probability $1-d$:

$x_{i,t+1} = x_{j,t}; x_{j,t+1} = x_{j,t}${donor, j, selected randomly from dyad}

With probability d:

$x_{i,t+1} = z_t; x_{j,t+1} = x_{j,t}${randomly selected member of dyad, i, takes behaviour z_t}

In the categorical-error formulation, z_t is a randomly chosen category of behaviour, so that occasionally one of the animals adopts another form of behaviour, present in the population but not necessarily previously used by either of the interactants. In the categorical-innovation formulation, z_t is a new category of behaviour, unused by any other individual at that time. d is the learning error in the first case, and the innovation rate in the second.

With categorical behaviour, the behavioural diversity was measured by Shannon's information index which ranges between 0 (all behaviour in one category) and $\log(q)$ (equal numbers of individuals in each category):

$h' = -\Sigma p_k \log(p_k)$

where p_k is the proportion of individuals with behaviour category k.

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[1] The categorical equivalents of the averaging and directional transfer methods were (assuming ordinal ranking of categories): With probability $1-d$: Averaging: $x_{i,t+1} = x_{j,t+1} = |(x_{i,t} + x_{j,t})/2|$ {nearest integer to mean of $x_{i,t}$ and $x_{j,t}$}. Directional transfer: $x_{i,t+1} = x_{j,t}; x_{j,t+1} = x_{j,t}$ {donor, j, has $x_{j,t} > x_{i,t}$}. With probability d: Averaging: $x_{i,t+1} = x_{j,t+1} = z_t$ {z_t is randomly chosen integer between 1 and q} Directional transfer: $x_{i,t+1} = x_{j,t}; x_{j,t+1} = x_{j,t}$ {$x_{j,t} > x_{i,t}$; individual with "lowest" behaviour, i, takes random behaviour}.

1.3. Social structures

We first made the simulations on a "random" social network, with each a_{ij} chosen randomly from the uniform distribution on the interval [0.1].

In the second set of simulations, which mimics social structures with permanent, but non-territorial, social units (e.g. African elephants (*Loxodonta africana*), killer whales, sperm whales), individuals within a population were allocated, randomly, to g units, and then associations between members of the same unit were chosen from the uniform distribution on the interval [0,1], and those between members of different units chosen from the uniform distribution on the interval [0,μ]. If $\mu=1$, then this reduces to the random network model. For each population the social differentiation was measured by Newman's (2004) modularity, defined as the difference between the proportion of the total association within clusters and the expected proportion when individuals associate randomly. Modularities near zero (generally from runs with $\mu > \sim 0.5$) indicate no particular clustering of the population, modularities greater than about 0.3 (roughly equivalent to $0.2 > \mu > 0.05$, depending on other parameters) suggest real social divisions in the population (Newman, 2004), and those near 1.0 (produced with values of μ near 0.0) a highly compartmentalised population. The modularity for any simulated population was calculated for the division of the population into clusters chosen by Newman's (2006) eigenvector method. This division was not necessarily the same as that of the simulated units, although with high modularity (and low μ) they almost always coincided.

The third set of simulations considered range-based social systems, in which each animal has a distinct spatial range, and associates more often with individuals whose ranges most overlap (such as orang-utans (*Pongo* spp.), many cervids). In these runs the centroids of the ranges of the members of the population were placed randomly on a square with sides of 1 unit. The association index between two individuals with centroids r_{ij} units apart was then

$a_{ij} = e^{-\beta r_{ij}}$

In this formulation, β indicates the ranging behaviour of the individuals. With high β, associations are primarily between individuals with range centroids in close proximity, whereas with low β associations are less dependent on range overlap and more even across the population (see Fig. 1). As with the unit-based social systems, modularity was calculated for each association matrix.

1.4. Running the models

For socially unstructured populations (i.e. without social units or spatial structure) we made 100 runs of the model with all combinations of the following model settings and parameters:

1. Continuous behaviour, categorical behaviour with error, categorical behaviour with innovation.
2. For continuous behaviour
   each of the three exchange mechanisms: averaging, random, directional.
   For categorical behaviour
   $q=3, 9, 27$ initial categories.
3. Population sizes $N=10, 50, 100$.
4. Learning errors $d=0.00, 0.01, 0.02, 0.05$.

We used the results of these models to see how the different model formulations and parameters affected the time until behavioural diversity reached an approximate equilibrium, the
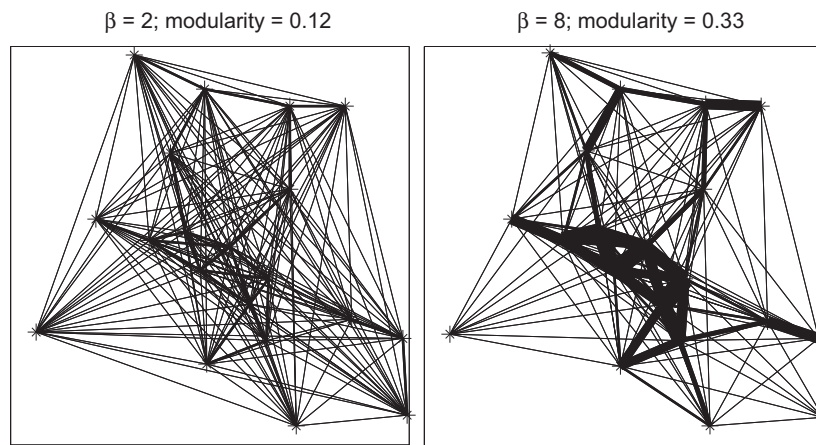
Fig. 1. Illustration of spatially based social structures. Both plots show the centroid positions of the same 20 individuals. These centroids are joined by lines whose widths are proportional to the association indices between the corresponding individuals. Lines are not shown for pairs of individuals with association indices less than 10% of the overall average association. The associations on the left were calculated with $\beta=2$ and those on the right with $\beta=8$.

diversity after this equilibrium, the trend in mean behaviour after equilibrium diversity for continuous behaviour, and the number of final categories with categorical behaviour.

After some experimentation, we found that if the number of encounters used was ten times the number of dyads (i.e. $10N(N-1)/2$, where N is the number of individuals), the output measures half way through a run were good predictors of those at its end. We used this formulation to set the number of encounters for each run. Trajectories of mean value (for continuous behaviour) and diversity are shown for sample runs in the Supplementary data.

We attempted to find functions which described the behavioural diversity at the end of the run as a function of the population size (N) and rate of learning error (d, only considering cases where $d > 0$), using the Akaike Information Criterion to select models (Burnham and Anderson, 2002).

We then socially structured the populations using both the unit-based and spatial methods described above. For each set of values of the parameters of the social system ($g=2$, 5, 10, 20 and $\mu=0.0125$, 0.025, 0.05, 0.1, 0.2, 0.4, 1.0 for the unit-based systems; $\beta=1.0$, 1.4, 2.0, 2.4, 4.0, 5.7, 8.0, 11.3, 16.0, 22.6, 32.0 for the range-based ones), we made 40 runs each with all the combinations of model settings and parameters listed above for the unstructured populations (except $d=0.02$, as the unstructured runs indicated a fairly simple relationship between diversity and d). We present the results of these simulations by plotting behavioural diversity at the end of the runs (mean over final 10% of time periods) against the modularity of the social system (m), and looked for modifications of the functions describing behavioural diversity which we had obtained from the results of the unstructured model, so that diversity in structured societies might be predicted using modularity, and possibly other parameters.

2. Results

2.1. Temporal trajectories of behaviour over random social networks

The initial runs used a random social network, with the association indices between pairs of individuals (a_{ij}'s) chosen randomly from the uniform distribution on the interval [0,1]. In Fig. 2 we plot measures that describe the characteristics of the trajectories of these simulations, and the third column of Table 2 gives the best-fit models of diversity.

The three mechanisms by which individuals exchanged continuous information produced characteristically different trajectories.

As might be expected, with behavioural values averaged at each encounter, the mean value over the population was very stable, keeping close to its original value (Supplementary data). Variation in behavioural value within the population generally decreased over about the first $5N$ encounters and then stabilized with a standard deviation of about twice the SD of the learning error, d (Fig. 2A, B), although increasing slightly with population size (Table 2). With random selection of the direction of information transfer between animals encountering one another, the mean continuous behavioural value varied considerably over time, but especially over about the first N^2 encounters (Fig. 2A; Supplementary data). In this scenario, the behaviour was unpredictable, and the diversity often large (Fig. 2B), but generally increasing proportionately with learning error, d, and roughly the squareroot of the population size, N (Table 2). With directional transfer of information from individuals with higher behavioural value towards those with lower behavioural value, population means for continuous behaviour trended upwards at a rate of approximately $1.3d/N^{0.87}$ per time unit (function fitted by eye to data in Fig. 2C), so at a rate roughly proportional to the learning error and decreasing with population size (Fig. 2C). In a manner comparable to the results with averaging, variation in behavioural value within the population generally decreased over about the first $5N$ encounters and then stabilized with a standard deviation roughly proportional to d, and decreasing somewhat with population size (Fig. 2A, B; Table 2).

We also experimented with mixed methods of transferring continuous behavioural information, so, for instance, having random transfer with probability 0.8, and directional transfer with probability 0.2. The results with these mixed methods were as might be expected from the original runs summarised in Fig. 2A–C. With a decreasing frequency of random transfer, the trajectory became more stable more quickly, and with a decreasing frequency of directional transfer, the rate of increase of the mean behavioural value also decreased.

With categorical behaviour, and random transfer, the time to equilibrium diversity was roughly N^2 encounters (Fig. 2D), as in the case of continuous behaviour with random transfer. However, compared with continuous behaviour, diversity, as measured by Shannon's information index, was less affected by the amount of learning error (d) and more by population size (N), increasing as roughly the squareroot of their product (Fig. 2E; Table 2). With innovation in categorical behaviour, the number of initial categories had little bearing on the behavioural diversity, but with error in the transfer of categorical behaviour diversity increased with number of initial categories. Except when there was no
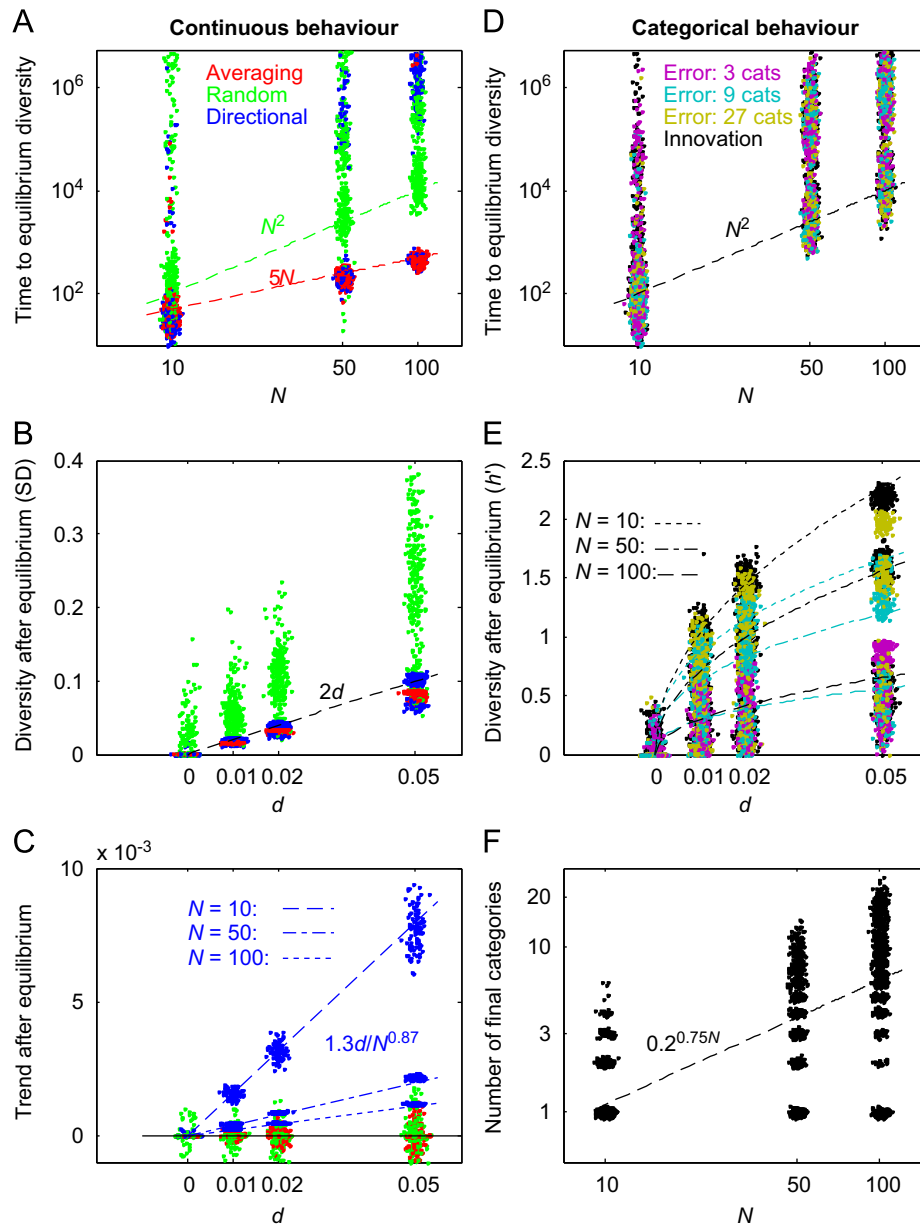
Fig. 2. Measures of the trajectories of the diversity of continuous behaviour (A–C) and categorical behaviour (D–F) with 100 simulations for each set of parameter combinations. Plotting symbols are jittered to lessen overlay on one another. For each trajectory, the simplex method was used to fit the function: diversity $= a + be^{-\lambda t}$. The approximate time to equilibrium diversity (A, D) was estimated by $1/\lambda$, and the equilibrium diversity (B, E) by the mean diversity over the final 10% time periods. The trend in diversity (C) with continuous behaviour was estimated from the slope of a linear regression of diversity against time from $3/\lambda$ time units to the end of the simulation. With innovation of categorical behaviour, we plot (F) the number of behavioural categories at the end of the run against the population size. The functions shown by lines on panels (A–F) are fitted by eye to the data, and are illustrative only. Those in panel (E) are from the fitted functions (given in Table 2, column 3) for categorical behaviour with error and 9 initial categories (cyan) and categorical behaviour with innovation (black).

Table 2
Fitted models of the diversity of behaviour for continuous (with averaging, random and directional transmission) and categorical (with error or innovation, and different numbers of initial categories) behaviour without social structure as functions of learning error, d, and population size, N, (column 3), and multipliers for situations with social structure based on either social units or spatial location, as functions of modularity, m, (columns 4–7).

Behaviour	Transmission/categories	Fitted model	Unit-based structure, multiplier:		Space-based structure, multiplier:	
		No structure	Formula	$m=0.8\ N=50$	Formula	$m=0.8\ N=50$
Continuous	Averaging	$1.51.d.N^{0.02}$	$\exp(1.05.m^{-1.76+1.60\log(N)})$	1.5	$\exp(2.66.m^{-1.76+1.60\log(N)})$	2.7
Continuous	Random	$0.83.d.N^{0.44}$	$\exp(0.92.m^{-0.51+1.08\log(N)})$	1.5	$\exp(2.00.m^{-0.51+1.08\log(N)})$	2.4
Continuous	Directional	$1.13.d.N^{0.14}$	$\exp(1.37.m^{-1.08+0.96\log(N)})$	2.1	$\exp(5.14.m^{-1.08+0.96\log(N)})$	16.9
Categorical (error)	3 categories	$0.49.d^{0.32}.N^{0.35}$	$\exp(0.37.m^{-3.84+2.16\log(N)})$	1.1	$\exp(0.80.m^{-3.84+2.16\log(N)})$	1.3
Categorical (error)	9 categories	$0.63.d^{0.40}.N^{0.47}$	$\exp(0.52.m^{-4.70+2.41\log(N)})$	1.2	$\exp(0.96.m^{-4.70+2.41\log(N)})$	1.4
Categorical (error)	27 categories	$0.80.d^{0.45}.N^{0.49}$	$\exp(0.38.m^{-3.30+1.70\log(N)})$	1.2	$\exp(0.79.m^{-3.30+1.70\log(N)})$	1.5
Categorical (innovation)	All categories	$0.82.d^{0.49}.N^{0.54}$	$\exp(0.46.m^{-4.07+2.16\log(N)})$	1.2	$\exp(1.01.m^{-4.07+2.16\log(N)})$	1.5

learning error ($d=0$) and so no innovations, innovations increased the number of categories to roughly $0.2N^{0.75}$ (Fig. 2F), although generally more categories were achieved with greater learning error (not shown).

In general diversity was reasonably well predicted by functions of the form:

$$b_1 d^{b_2} N^{b_3}$$

where b_1, b_2 and b_3 are fitted parameters which differ between continuous or categorical behaviour, the modes of information transfer, and the number of initial categories for categorical behaviour with error. $b_2=1$ for continuous behaviour (Table 2). These functions are reasonable predictors of diversity, but not perfect. For instance, the prediction is a little high with random transfer of continuous behaviour and $N=10$ (Fig. 3), and with categorical behaviour, transmission with error, modularity ~ 0.8 and $N=100$ (Fig. 4).

2.2. Structured social networks

For continuous behaviour, the mean behavioural value at the end of the runs was little affected by structuring populations spatially or into units: means of the ratio between the final mean behavioural value for runs with modularity > 0.6 and those with modularity < 0.2 over the 12 combination of N and d and spatial or unit social structures were 1.00 for averaging, 1.02 for random, and 1.04 for directional transmission. However, the diversity of behaviour within the population generally increased with modularity for both continuous (Fig. 3) and categorical (Fig. 4) behaviour, except that with no learning error ($d=0$) almost all populations were homogeneous in behaviour, whatever the modularity. We found that the proportional increase in diversity with modularity could be reasonably well predicted by functions of the form (Table 2; Figs. 3 and 4):
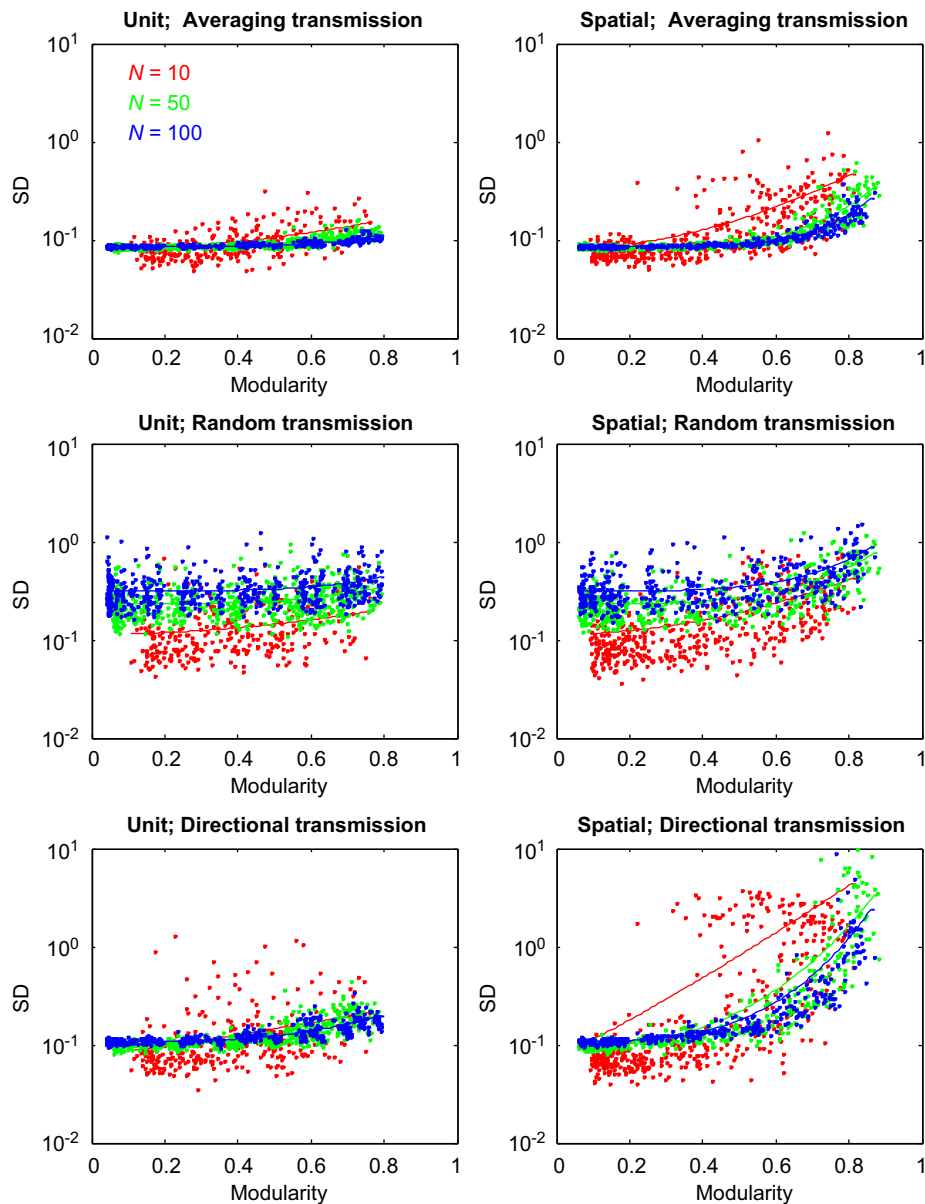
$$e^{c_1 m^{-c_2} + c_3 Log(N)}$$

Fig. 3. Diversity of continuous behaviour with modularity for unit-based social systems (left) and spatially based socially systems (right) with learning error of $d=0.05$. Also shown are the best fit models in each scenario from Table 2 (combining columns 3 and 4).
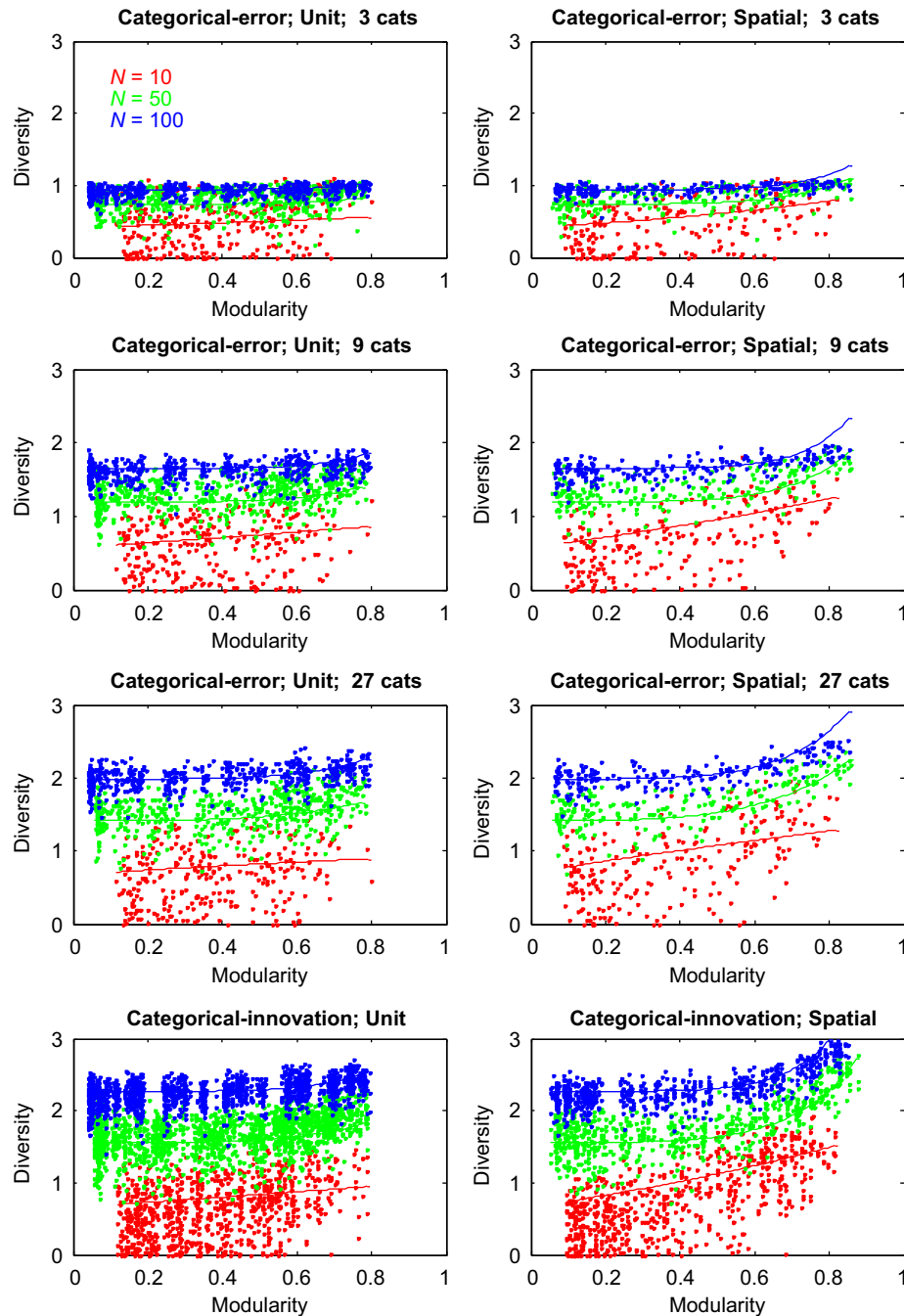
Fig. 4. Diversity of categorical behaviour with modularity for unit-based social systems (left) and spatially based socially systems (right) with learning error of $d=0.05$. Also shown are the best fit models in each scenario from Table 2 (combining columns 3 and 4 or 6). The first three rows give the results for transmission with error for 3, 9, 27 initial categories, and the final row categorical behaviour with innovation combining runs with all numbers of initial categories (as this did not affect the final diversity).

where c_1, c_2 and c_3 are fitted parameters which differ between unit/spatial social systems, continuous/categorical behaviour, the type of information transfer, and the number of initial categories for categorical behaviour with error. Thus diversity increases with modularity but the rate of increase depends on the type of behaviour, the kind of social learning, the form of the social system, and the population size (Table 2). For modularities of $m=0.8$, increases in diversity were slight with categorical behaviour and unit-based social structure, and much more substantial with spatially based structure and continuous behaviour (Table 2).

In small populations and with modularity greater than about 0.4, a subset of runs with continuous behaviour gave much higher diversity—roughly an order of magnitude higher in the case of

directional transmission—than the mode for that modularity (Fig. 3). These likely represent situations in which some clusters of individuals were virtually socially isolated from one another and so developed independent behavioural trajectories. The increase in diversity with modularity was greater for spatially based social systems, than unit-based ones (Table 2; Figs. 3 and 4). Spatially based social structures promoted highly heterogeneous behaviour when individuals primarily associated only with their close neighbours (high β and modularity). The diversity of continuous behaviour increased most clearly with modularity under directional transfer of information, and least obviously with random transfer (Table 2; Fig. 3). With continuous behaviour, there was a strong interaction between population size and

modularity: diversity increased faster with modularity in small populations compared with larger ones (Table 2; Fig. 3). This was not so apparent with categorical behaviour (Table 2, Fig. 4).

Increases in behavioural diversity with population modularity result primarily from independent behavioural trajectories in the increasingly socially isolated clusters into which the population is divided. To examine this we tested whether there were significant differences between the behaviour of animals in the different clusters identified by the modularity analysis using one-way ANOVAs for continuous behaviour, and chi-squared tests for categorical behaviour. When $N = 50$, $d = 0.01$, and 9 initial categories for categorical behaviour (using 10 runs with each combination of unit/ spatial social systems, continuous/categorical behaviour, the type of information transfer), tests usually (93%) showed significant ($P < 0.05$) differences in behaviour between clusters when modularity was greater than 0.6, differences were sometimes significant with modularities between 0.4–0.6 (53%) and 0.2–0.4 (25%), and rarely significant (9%) with modularity less than 0.2.

3. Discussion

Social structuring increases the diversity of culturally transmitted behaviour. However the effects are erratic. In some cases, as with the directional transmission of continuous behaviour there can be ten-fold increases in behavioural diversity among spatially structured populations, but with averaging transmission and unit structuring the increase is much more modest, even with the same degree of modularity (Fig. 3). Even with the same set of parameters governing social structure and behavioural transmission, behavioural diversity could be highly unpredictable (Fig. 3). In fact, even within the same run diversity could vary by a factor of three or more, especially with random transfer of continuous behaviour or categorical behaviour with innovation (Supplementary data).

It may be that there is some measure of social structuring that can predict the diversity of culturally transmitted behaviour better than modularity, and finding such a measure would be a useful goal of subsequent research. However the variation in diversity among runs with the same social and transmission parameters, and particularly the changes in diversity within runs, shows that the prediction of cultural behavioural diversity from any measure will often be imprecise.

Our null model was one of random association indices (links) between individuals. An alternative null would be uniform associations among individuals. Such a network would be simpler, and analytically tractable, but is not realistic. Some species, especially marine species, that are postulated to have important cultures, have fairly homogeneous social relationships at the lowest tier of their social structure. For instance Christal and Whitehead (2001) suggested that relationships are "quite homogeneous" within sperm whale social units. However, in one well studied sperm whale social unit, the coefficient of variation of the association indices between the non-infant members of the unit was 0.76 (Gero et al., 2008), a little larger than the expected value of 0.58 ($1/\sqrt{3}$) for our basal random networks. While there may be no realistic counterpart for a network with uniform edge weights, analyses using such networks can provide context for our results. For instance, on such a uniform network with an ordinal analogue of our random transfer of continuous behaviour, Lawson and Jenson (2007) found that behavioural diversity (measured as we did by the standard deviation of the behavioural value) was about $0.63d$ (adapting their Eq. (17)). The diversity with random transfer in the simulations on our more structured network was also roughly proportional to d, but with a slope depending also on the population size, N, that is greater than 0.63 (Table 2). This greater diversity is induced by the more structured

social system that we simulated. Similarly, Voelkl and Noë (2010) found that compared to a uniform social network, transmission over networks that mimic real primate social networks significantly altered spreading patterns, speed of transmission, and the robustness of information.

Our models show that when behaviour is socially learned, then behavioural diversity within a population increases with error in the learning process, when the direction of social learning is unpredictable rather than fixed, and with increasing social structure in the population. Thus, under these scenarios, behaviour is most diverse when most animals have the opportunity to learn from just a few other individuals who are themselves interconnected, and when the learning process is error prone and not structured. Modularized but rather egalitarian societies, such as those of killer and sperm whales (Ford et al., 2000; Whitehead, 2003), fit this sketch. Other studies have indirectly inferred that increased structural constraints will lead to increased diversity for other important processes taking place on social networks. Diversity in communication systems, e.g. linguistic diversity, will evolve in social networks if interactions between individuals are restricted either socially or spatially (Arita and Koyama, 1998; Ferrer i Cancho et al., 2005). A particularly large body of work has examined how genetic diversity is affected by population structuring. Although genetic transmission and the forms of social learning that we model are very different, as are the time scales being considered, there are some parallels in the most general conclusions. For instance changes in overall population genetic diversity due to population structuring are dependent on population size, the migration rate between subpopulations (which is an inverse analogue of modularity), and the mutation rate, which is an analogue of error in social learning (Amos and Harwood, 1998; Harrison and Hastings, 1996). However these effects can be complex and dependent on time scale (Allendorf and Luikart, 2007; Harrison and Hastings, 1996).

The predictions about the relationship between behavioural diversity and social structure that emerge from these models can potentially be tested by comparing species for which we have data on social structure and cultural behaviour. A preliminary literature review suggested that there is currently insufficient information to make such a test with any power among either the cetaceans or primates, but accelerating interest in the culture of wild animals may make such a test possible before too long. For example, we would predict that labile fission-fusion social structures would have a lower behavioural diversity than more socially constrained populations. Some cosmopolitan or widely ranging species such as bottlenose dolphins (*Tursiops* spp.) in which there are indications that directional social learning is important (Krützen et al., 2005; Rendell and Whitehead, 2001) could form the basis for an interesting test of these predictions in which the transfer mechanism can be assumed similar across all populations while the social structures differ substantially (Lusseau et al., 2003).

Does the behavioural diversity output from our models represent "culture"? Culture may be defined many ways (Mundinger, 1980), but in a recent edited volume entitled "The Question of Animal Culture" (Laland and Galef, 2009), the authors of all the chapters agreed that culture is behaviour transmitted by social learning and shared by members of a community. Some authors required additional conditions for culture beyond these two factors, but there was almost no agreement on what these additions should be. Thus there is a strong argument for adopting a definition of culture that includes just social learning and shared behaviour (see Laland et al., 2009). The behaviour that we have modelled is socially learned, but is it shared? It becomes increasingly shared as the modularity of the social structure itself increases (Figs. 3 and 4). This indicates that the "shared" requisite of culture is more a property of the underlying social structure

than of the behaviour (see also Nunn et al., 2009). Newman (2004) suggests that when modularity exceeds about 0.3 then there are important divisions in the population. In our models, behavioural diversity generally begins to increase at modularity coefficients above very roughly 0.3, although there is no sudden threshold (Figs. 3 and 4). So we conjecture that social learning produces culture in populations whose social structure has a modularity of about 0.3 or greater. We propose that above this threshold the reduced rate of interaction of individuals between communities will increase isolation between individuals that have different behavioural values. Therefore it represents an approximate level at which the imposed social structure out-weighs behavioural homogenisation through social learning between communities. The modularity at which diversity increases (about 0.3) does not appear to depend on learning error or the transfer mechanism imposed on the network, despite those factors being important drivers of the final diversity within each of our simulated networks. It therefore seems that social struc-tural constraints may have a dominant effect on the behavioural diversity that a network can realise.

We have modelled several simple social learning processes, which, as we have indicated in Section 1, have at least some putative basis in the real behaviour of animals. However, social learning will often be more complex (Rendell et al., 2011), even in non-humans. For instance, the probability of using social learning to learn behaviour may often be related to an individual's recent success in similar behaviour. Also we omitted one mechanism that is potentially important in shaping culture and then influen-cing behavioural diversity, conformism (Boyd and Richerson, 1985; Henrich and Boyd, 1998; Richerson and Boyd, 2005). If individuals preferentially adopt behaviour that is common in their community, then the consequences for evolution through group selection, as well as for population biology, can be profound (Henrich and Boyd, 1998; Richerson and Boyd, 2005; Whitehead and Richerson, 2009). Conformism is perhaps more likely to evolve in unit-based social systems rather than spatially based ones, and, as conformism within a modular population will tend to increase behavioural diversity, this may close the gap between the diversities of unit based and spatially based social systems with the same modularity. But how modular does the social structure need to be before this happens? This will depend on how conformity operates, on which population segment is being conformed to, and how rigorously. There are several reasonable possibilities, which is why we omitted conformism at this stage of the research programme. However adding conformism to our models is clearly a desirable step in gaining a theoretical under-standing of the relationship between social structure and culture.

Other potentially productive ways to enhance the model and make it more realistic might include adding temporal stochasticity to the social network, including birth and death processes, con-sidering asymmetries in information flow so that the probability of A learning from B is not necessarily the same as B learning from A (Nunn et al., 2009; Voelkl and Noë, 2008), and modelling multi-dimensional behaviour. We hope that our study might be one stepping-stone towards a model of the coevolution of social structure and culture, complementing studies such as those of Rosvall and Sneppen (2009) who show how social learning through a network may lead to group formation, and Bryden et al. (2011) whose simulations of dynamic binary networks showed that when connections between nodes are more likely to form between individuals possessing similar states, then stable communities are found. Our model might be extended to allow individuals to change their association indices $\{a_{ij}\}$ when encountering individuals or groups that have similar behavioural values, promoting behavioural homogeneity within groups, and probably population-wide beha-vioural diversity. While this process is readily understandable and

sometimes evident in human societies (Bowles et al., 2003), it may be more difficult to envisage with non-humans. However, such mechanisms can help explain the lack of dispersal from natal groups for populations exhibiting a diversity of group-specific foraging specialisations in which spending time with individuals that have different foraging tactics may lead to reduced food intake. Indeed for behavioural values that have close links to individual fitness the coevolution of social structure and culture can be readily explained as an individual selection process.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2011.10.025.

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