Full Model Description
premo_2012.nlogo
Updated in 2018 to run on NetLogo 6.0.2.

This model description follows the guidelines of the ODD protocol (Grimm et al. 2010). This model was used to collect the data presented in Premo (2012). Note that the original version of this model was run on NetLogo 4.1.1. The original code, which is no longer compatible with later versions of NetLogo, is still available upon request from the author. The code was updated in 2018 to run on NetLogo 6.0.2. Note that the present version of the code may need to be modified further to run on subsequent versions of NetLogo.

Purpose
This model is designed to address the following research question: How does the amount and topology of intergroup cultural transmission modulate the effect of local group extinction on selectively neutral cultural diversity in a geographically structured population? The experimental design varies group extinction rate, the amount of intergroup cultural transmission, and the topology of intergroup cultural transmission while measuring the effects of local group extinction on long-term cultural change and regional cultural differentiation in a constant-size, spatially structured population. The results show that for most of the intergroup social network topologies tested here, increasing the amount of intergroup cultural transmission (similar to increasing gene flow in a genetic model) erases the negative effect of local group extinction on selectively neutral cultural diversity. The stochastic (i.e., preference attachment) network seems to stand out as an exception.

Entities, state variables, & temporal and spatial scales
The model employs two classes of agents: individuals (turtles) and groups (patches). Individuals serve as the vehicles of cultural transmission. Individuals have only 2 variables: one representing whether they are members of the experienced or naive generation (*age*) and one representing a selectively neutral cultural variant (*culturalVariant*). The *age* variable can be assigned one of two possible values: 0 (born during the current time step) or 1 (born during the previous time step). *culturalVariant* can take the value of any integer, positive or negative. Individuals have only two methods: *die* and *cultTransmission*. An individual dies if its group goes extinct or if its *age*=1 after the completion of unbiased cultural transmission within groups. The method, *cultTransmission*, defines the way in which each "naïve" individual acquires its *culturalVariant* from a randomly chosen member of the "experienced" generation (i.e., an individual with *age*=1) within its group.

In the context of this model, groups are best described as spatially explicit containers of individuals. Groups provide the population with spatial structure. Each group is characterized by a unique Cartesian coordinate as well as *linkedPatches*, *modeCulturalVariant*, *H*, *ShannonsIndexGroup*, *differenceFromAncestral*, *differenceToAllOtherGroups*, *withinGroupDiversity*, *fissions*, and *extinctions*. Groups have the following methods: *intergroupTransmission*, *colonize*, *calculateWithinGroupPortionOfHt*, *calculateDifferenceFromAncestral*, and *calculateDifferenceToAllOtherGroups*.

The model proceeds in simulated time steps (time steps are called "ticks" in NetLogo). Each time step represents a single non-overlapping generation. That is to say, by the end of each time step, the entire "parental," or experienced, generation—those individuals alive at the beginning of the time step—has been replaced by a new generation of "offspring," or naïve, individuals. Note the non-overlapping generations aren't meant to represent actual human generations, but rather the time needed for 2 things to happen: 1) a cultural trait is passed from experienced practitioners to naive students within groups and 2) *Nm* individuals in each group replace the *culturalVariant* they adopted through unbiased cultural transmission with the *culturalVariant* they acquire through horizontal transmission between groups.

The model is spatially explicit. The spatial environment is a grid of regularly spaced and shaped square cells. The edges of the grid are wrapped into a torus to avoid edge effects. Although cell size does not equate to an empirical value, one can think of it as the area needed to support the subsistence activities of a single social group within an idealized homogeneous landscape. Thus, each cell represents a single group, which can contain up to *maxGroupSize* individuals.

Process Overview and Scheduling

Each time step is composed of 6 distinct processes, which occur in the following order: individuals age, groups are exposed to risk of local extinction, the naive generation is created, cultural variants are transmitted from the experienced generation to the naive generation within groups, the experienced generation is culled, and intergroup cultural transmission occurs among members of the naive generation.

First, at the very beginning of each time step, each individual (i.e., turtle) changes the value of its age variable from 0 to 1 to reflect the fact that it is now a member of the "experienced" generation and can serve as a teacher during unbiased cultural transmission later in the time step.

Second, each group (i.e., patch) is exposed to local extinction and recolonization. If a real number chosen randomly from a uniform distribution bound by 0 and 1 is less than *groupExtinctionProb*, then the individuals who are members of that group are removed from the simulation immediately. Following a local extinction event, the cell is empty. Each empty cell is repopulated with members of the experienced generation taken from a randomly chosen neighboring cell when *localReplacement* = true or from a randomly chosen cell when *localReplacement* = false. Empty cells begin to be repopulated only after all groups have been exposed to a chance of local extinction.

Third, the naive generation is created; 25 new individuals are created in each group. Members of the naive generation are distinguished from those in the experienced generation by age (*age*=0 for naive generation, *age*=1 for experienced generation).

Fourth, each member of the naive generation undergoes unbiased cultural transmission within its group. Unbiased cultural transmission involves (1) learning from a teacher who is drawn randomly (with replacement) from among the members of the experienced generation within the same group and (2) being exposed to the probability (*errorProb*) of making an error when

copying the teacher's *culturalVariant*. Copy errors always result in the naive individual adopting (with equal probability) either x-1 or x+1 as its *culturalVariant*, where x represents the value of the teacher's *culturalVariant*. This is the *bidirectional* version of the single stepwise mutation model. See Submodels for more details on cultural transmission and copy errors.

Fifth, all remaining members of the experienced generation (i.e., *age*=1) are culled from the simulation. The population size (2500) is the same as it was at the beginning of the time step, but now all of the individuals are members of the naive generation (i.e., *age*=0).

Sixth, *Nm* individuals in each group undergo horizontal intergroup cultural transmission. "*N*" refers to the maximum number of individuals in the group and "*m*" refers to the probability of learning via intergroup cultural transmission. Intergroup cultural transmission involves each of the *Nm* individuals in each group learning from a teacher who is drawn randomly (with replacement) from among the members of the naive generation in a group that is "linked" to the learner's group. The topology of the intergroup social network can take one of four forms: global (essentially the teacher is chosen randomly from any group that is not the learner's), spatial (the teacher is chosen randomly from any of the groups that are located within *intergroupTransmissionRadius* of the learner's group), stochastic network (the teacher is chosen randomly from any group that is linked the learner's group in a preference attachment network), or small world (the teacher is chosen randomly from any group that is linked the learner's group in a small world network with *rewireProbability*=0.2). Note that, unlike the case of unbiased cultural transmission within groups, intergroup cultural transmission does not include copying error. Please see *intergroupTransmission* in Submodels for more details.

Design Concepts

Evolution. In the context of this model, evolution refers to change in cultural variant frequencies in a population through time. Because the cultural trait is selectively neutral in this model, the results speak only to neutral cultural evolution.

Stochasticity. Stochasticity is incorporated into many aspects of this nondeterministic model: copy errors and localized group extinctions are represented probabilistically, agent order is randomized before every process, teachers are chosen randomly from among the set of candidates, and the groups tabbed to fission in order to repopulate an empty group are chosen randomly from among the empty group's Moore neighbors. The small world and preference attachment social networks also include stochastic elements.

Initialization

At the start of each simulation, all groups (100) possess the maximum number of individuals (25), for a total of 2500 individuals. When *equilibrium*=False, every one of these individuals displays *culturalVariant*=0 at the start of the simulation run. Under this condition, the initial population is perfectly homogeneous in terms of cultural diversity; there is no variation within or between groups. When *equilibrium*=True, every individual displays a *culturalVariant* value chosen at random from a uniform distribution of integers between 0 and 10^8. Under this condition, the initial population is heterogeneous in terms of cultural diversity and there is

maximum variation within and between groups at the start of the run. Table 1 provides the values used to initialize the simulations reported in the paper.

Table 1. Parameter values used to initialize the simulations reported in Premo (2012).

Standard parameters	
maxGroupSize	25
errorProb	0.001
innovationType	bidirectional
intergroupTransmissionRadius	1
rewireProbability	0.20
localReplacement	True
equilibrium	True, False
Experimental parameters	
groupExtinctionProb	0, 0.001, 0.01, 0.1
Nm	0, 1, 2, 3, 4, 5
intergroupTransmissionType	spatial, global, stochastic, small world
seed	1-20

Input Data
The model does not require any input data or additional files to initialize a simulation run.

Data Collection
Data are collected from each simulation after 50,000 time steps. I collect variant richness (the total number of unique cultural variants displayed by the entire population), total diversity (H_T), within-group diversity (H_S), F_{ST} (the proportion of total diversity explained by between-group diversity), $\bar{d}_G$, and $d_{A\,max}$. Please see Premo (2012) and the source code for the formal definitions of these measures of cultural variation, group differentiation, and rates of cumulative change.

Submodels
Creating a scale-free stochastic social network (*establishLink*):
This is a patches method used to create a stochastic (i.e., preference attachment) network, as described in Bentley and Shennan (2003). The general idea here is that, as the social network is created, the likelihood that a link is created between a newly added unlinked node and any extant node is a function of the number of links at the extant nodes. This is a rich-get-richer type of network in which nodes with more links are more likely to attract additional links than nodes with fewer links.

Each patch goes through these steps after it adds 25 turtles at the start of a simulation run.
1. All other patches that contain turtles are added to a local agentset called *possibleLinks*.

2. Each member of *possibleLinks* adds its *plabel* to *tempList* X times, where X represents the number of links it currently has. For example, a patch with *plabel* = 3 that is linked to 5 other patches would add the number "3" to *tempList* 5 times while a patch with *plabel* = 4 that is linked to 2 other patches would add the number "4" to *tempList* 2 times.
3. After all of the members of *possibleLinks* have populated *tempList* with their *plabel*s in quantities that correspond to the number of links they currently have to other patches, then one item is randomly chosen from *tempList*. This item represents the *plabel* of the patch to which ego will be connected via a link in the social network. The link is created by setting ego's list of *linkedPatches* to include the patch that matches the *plabel* drawn from *tempList* and by asking the newly linked patch to add ego to its list of *linkedPatches*.

Recolonizing empty cells (*colonize*):
As described above, when a group undergoes a localized extinction event, all of the individuals within it are removed from the simulation. To repopulate the newly empty cell with some members of the experienced generation who will serve as possible teachers for the group's naive generation, a group from the empty cell's Moore neighborhood is randomly chosen to fission. Aside from being adjacent to the empty cell, the only other requirement for serving as a source of individuals is that the group must have at least 2 members. Once chosen, the group sends half of its individuals (chosen randomly from the agents in the cell) to "recolonize," or repopulate, the empty cell. These "colonizers" will serve as the experienced generation in the cell to which they have moved.

Unbiased cultural transmission within groups (*cultTransmission*):
Intergenerational cultural transmission occurs within spatially defined groups. Every unbiased cultural transmission event involves a naive "offspring" who has yet to adopt a *culturalVariant* and an experienced teacher from the "parental" generation. The naive individual copies the *culturalVariant* expressed by its teacher. Each naive individual randomly chooses its teacher (with replacement) from the set of individuals who are members of the "parental" generation in the naive individual's spatially defined group.

Unbiased cultural transmission is imperfect. A naive individual makes a mistake when copying its teacher's variant with probability *errorProb*. Each copying error results in the naive individual adopting a cultural variant that is one integer greater or lower (with equal probability) than the value it was trying to copy from its teacher. In the parlance of population genetics, the effect of copy errors on cultural variants follows a *bidirectional* single stepwise mutation model. The model also allows one to investigate a unidirectional, or *forward-only*, single stepwise mutation model.

Intergroup cultural transmission (*intergroupTransmission*):
Intergroup cultural transmission occurs between members of different groups. Put simply, each instance of intergroup cultural transmission is marked by a member of one group adopting the *culturalVariant* of a member of a different group. This occurs *Nm* times for each group during each time step. Most of the code in this submodel is used to delineate from which groups one's teacher can be drawn, as this is based on the topology of the social network that connects groups.

When *intergroupTransmissionType=spatial*, each "learner" in a group chooses its teacher randomly (and with replacement) from among the other groups (patches) that are located within the distance given by *intergroupTransmissionRadius*. Note that the subset of groups from which the learner may choose a teacher (*linkedPatches*) doesn't include the learner's own group. When *intergroupTransmissionRadius*=1, as it does in Premo (2012), this equates to the learner choosing a teacher from one of its von Neumann neighbors. This is referred to as the "local" social network topology in Premo (2012).

When *intergroupTransmissionType=global*, each "learner" in a group chooses its teacher randomly (and with replacement) from among the members of any other group. The only group from which the learner may not choose a teacher is its own group. This topology represents the idealized case in which all groups are equally connected to all others and the spatial distance between groups plays no role.

When *intergroupTransmissionType=stochastic network*, each "learner" in a group chooses its teacher randomly (and with replacement) from among the groups (patches) that are members of its group's *linkedPatches* list. Note that each group's *linkedPatches* list does not include itself—i.e., a group cannot be "linked" to itself in an intergroup social network.

When *intergroupTransmissionType=small world*, each "learner" in a group chooses its teacher randomly (and with replacement) from among the groups (patches) that are members of its group's *linkedPatches* list. Note that each group's *linkedPatches* list does not include itself—i.e., a group cannot be "linked" to itself in an intergroup social network. In the case of the small world network, each group's *linkedPatches* list is defined only after all groups have been initialized at the start of the simulation. The small world social network topology makes use of the global variable, *rewireProbability*. *rewireProbability* represents the proportion of patches that will reset, or "rewire," one of its links such that it replaces a link to a von Neumann neighbor with a link to a patch that is not a von Neumann neighbor.

In this model, intergroup cultural transmission does not include copying error.

Noteworthy model assumptions

This model does not allow for horizontal cultural transmission within groups. Naive individuals can only learn from members of the previous generation—never from members of their own generation—within their own group. It is unclear how including horizontal transmission within groups would affect the results, and this might be worth investigating further. Although intergroup cultural transmission is a form of horizontal cultural transmission, this occurs between members of different groups. Intergroup cultural transmission does not include copying error.

References

Bentley, R. A. and S. J. Shennan (2003) Cultural transmission and stochastic network growth. *American Antiquity* 68:459-485.

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Contact information

This model was programmed by Luke Premo (Department of Anthropology, Washington State University and the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology). One of the best things about computer simulation programs is that they can often be improved with the help of other researchers. The more sets of eyes that pass over the code, the better. So, please, have a look at the commented source code under the "info" tab. Any comments, questions, or corrections are always welcome. Feel free to contact me at:

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