Living in Enclaves

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What are the consequences of living in small isolated communities vs living in larger environments as members of bigger communities? If the resources are scarce and highly spatially and temporally variable, living in isolated communities can lead to extinction because of temporary food scarcity and less efficient genetic selection. Artifacts that increase the energy extracted from natural resources can avoid extinction of local populations, but still choosing the artifacts to be reproduced from the restricted artifact pool of the local community rather than from a larger pool leads to less good artifacts and smaller global population size.

Key Words: evolution of technology, cultural isolation, simulation of evolution

INTRODUCTION

Spatial structure is an important variable in the life of organisms. For example, population dynamics depends on spatial structure, which therefore is fundamental for many questions in ecology and conservation [1]. In human beings spatial structure (e.g., of settlements) may influence social interaction, cultural transmission, and the exchange of resources. Human groups can live in relative isolation due to physical or socio-cultural factors, or they can live in a large, shared environment in which individuals are free to move around and to obtain artifacts produced in distant portions of the total environment.

In this research we contrast two populations of organisms, a single-island population and a meta-population composed of subpopulations living in isolated islands. The results obtained when one contrasts single-island populations with meta-populations may depend on the type of phenomena under study. Ellner et al. [2], using both real experiments and computer simulations, have shown that predator and prey populations (prey mites and predator mites living on plants) tend to collapse in single-island populations, whereas meta-populations exhibit long-term persistence of both prey and predator populations more frequently. They explain this result by the fact that in the meta-population predators are less likely to detect prey outbreaks that may occur in a different "island," and this allows the prey population, and as a consequence also the predator population, to avoid extinction.

In humans things may be different. Enclaves defined as isolated local environments can result from a variety of factors. One is geographical isolation: living on a distant island without adequate seafaring technology that would make it possible to leave the island or living in a territory surrounded by high mountains. Another is political/cultural isolation, which intentionally cuts all links to the external world. Diamond [3] refers to precolonization Tasmania as an example of geographical isolation and to Japan before European contacts in the 19th century as an example of political/cultural isolation. In both cases living in enclaves tends to have negative consequences, for example, in terms of technological evolution.

We use a simulation scenario similar to Epstein and Axtell's Sugarscape [4] and Forrest and Jones' Echo [5] to study a population of organisms living and reproducing either in enclaves (i.e., a meta-population composed of subpopulations living in separate "islands") or in a common environment (a single-island population). The resources existing in the environment that allow these populations to survive and reproduce are highly variable both spatially and temporally. In these conditions living in enclaves is associated with a higher probability of population extinction. Furthermore, even if the presence of artifacts makes population extinction less probable in the population living in enclaves because artifacts allow the organisms to extract more energy from the resources present in the environment, the quality of artifacts—which evolve together with the organisms—is less good in the population living in enclaves than in the population that is free to move and to copy artifacts produced in the entire environment.

POPULATIONS WITH AND WITHOUT ENCLAVES

A population of organisms lives in an environment that contains randomly distributed food elements. At birth each individual possesses some energy that is reduced by some fixed amount at each time step. If the energy goes to zero, the individual dies. To reintegrate the lost energy and to remain alive, the individual must be able to approach and eat the food elements.

There are two such populations of organisms. In one population the individual organisms are free to move in the entire environment. The environment of the other population is divided up into a number of separate enclaves, and an individual that is born inside one enclave cannot leave the enclave. Our first question is: What are the consequences of leaving in enclaves?

Details of the Simulation

The total environment is a grid of 100 × 100 = 10,000 cells. At the beginning of the simulation 4,000 food elements are randomly distributed in the environment, with one cell carrying a single food element. One thousand food elements are periodically reintroduced each N time steps, where N varies randomly in the interval between 44 and 49 time steps, to compensate for food eaten. The initial population includes 100 individuals randomly positioned in the environment with one individual per cell. Each individual is born with N energy units, where N is randomly selected in the interval between 200 and 300. This energy is decreased by one unit at each time step, and when the energy goes to zero, the individual dies. However, when an individual enters a cell containing a food element, the individual eats the food (which disappears), and its energy is increased by 10 units. All individuals die at a maximum age of 300 time steps. As long as an individual succeeds in remaining alive, it periodically generates a single offspring each 50 time steps, and it gives half of its current energy to the offspring. The offspring is positioned in a randomly selected cell at a maximum distance of five cells from its (single) parent.

The behavior of each individual is controlled by a neural network, with two input units encoding the presence and location of the nearest food element within a maximum distance of 10 cells from the individual, two output units encoding one of four possible actions ("move one cell forward in the current facing direction," "turn 90 degrees to the left," "turn 90 degrees to the right," "do nothing"), and three hidden units linking the input to the output units. At each time step the individual is informed about the position of the nearest food element, and it responds with some movement. When the movement causes the individual to enter a cell containing a food element, the food element is eaten and the energy of the individual is increased by 10 units.

The connection weights of the 100 networks of the initial population are determined by randomly selecting a value in the interval between −3 and +3 for each weight. When an individual generates an offspring, the offspring inherits the connection weights of its parent, but all the weights are slightly mutated by adding a quantity randomly selected in the interval between −0.1 and +0.1 to their current value.

We have run six replications of two simulations. In one simulation there is no change in the environment until the end of the simulation, and the simulation is terminated after 25,000 time steps. In the other simulation, when population size has reached a value of 200 individuals (this is a more or less stable value approaching the carrying capacity of the environment), there is a sudden change in the environment. The total environment of 10,000 cells is divided up into 5 × 5 = 25 enclaves of 20 × 20 = 400 cells each. Each enclave is surrounded by a wall that prevents the individuals inside the enclave to leave the enclave. Furthermore, when an individual generates an offspring, the offspring is always positioned inside the enclave of its parent. Hence, the individuals that at the time the enclaves are created find themselves inside one particular enclave constitute a subpopulation that will never be able to leave the enclave. The simulation is terminated after 25,000 time steps like the first simulation.

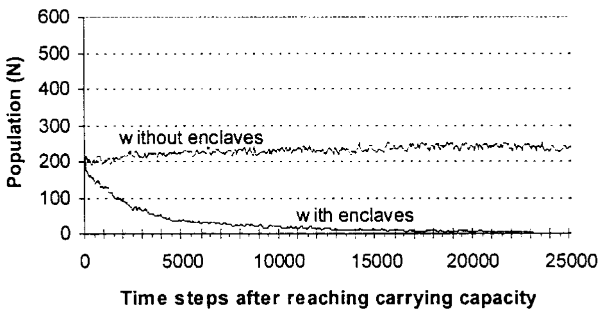
Results

What happens to the small populations living in the enclaves compared with the larger population free to move in the entire environment? The answer is quite straightforward. A population made up of subpopulations living in separate, isolated environments tends to become extinct. Although the size of the population that lives in the larger shared environment without enclaves remains more or less constant after reaching the carrying capacity of the environment, the size of the population made up of subpopulations living in isolated enclaves tends to decrease until it reaches the value of zero in all six runs of the simulation (Figure 1).

What causes population extinction in the population living in isolated enclaves? Two causes can be hypothesized. One cause is ecological. The environment is spatially and temporally heterogeneous from the point of view of food distribution. Because at each seasonal reintroduction ("year") food is randomly distributed, at any given time some parts of the environment are likely to contain less food than other parts. This will probably be a temporary condition but even temporary food scarcity, if sufficiently severe, can lead to extinction of the local population.

Spatial and temporal heterogeneity in food distribution means that at least for some period of time a particular portion of the environment can contain little food. In the population without enclaves this may cause no adverse effects because the individuals that happen to find themselves in a portion of the environment with little food are free to move to another portion of the environment with more food. For the population with enclaves, however, the situation is different. If a subpopulation finds itself in an enclave with little food, the individuals cannot leave the enclave and, if food scarcity is severe and somewhat prolonged, the result can be that the individuals die before they are able to generate offspring. Hence, the subpopulation living in that enclave becomes extinct. In fact, an analysis of the quantity of food reintroduced in each enclave in each "year" shows that there is a tendency for less than average food to be reintroduced in the "year" of extinction in the enclaves in which extinction occurs. The process is cumulative. Because enclaves in which the subpopulation living there has become extinct cannot be repopulated by other individuals even if the enclave is repleted with food the next "year" (as is likely to be the case because no one is eating the food present in the enclave), for purely chance reasons more and more enclaves will successively lose their inhabitants until the entire population becomes extinct.

FIGURE 1



Changes in population size for populations with and without enclaves. (Average of six runs for each type of population.)

The second cause of extinction in the population made up of subpopulations living in isolated enclaves appears to be genetic. In our simulations the ability to find food is genetically inherited. We can measure the ability possessed by particular individuals by testing each individual in identical controlled conditions. Using this method we find that, before the introduction of the enclaves, the two populations have the same average level of eating ability. However, if we measure eating ability after 16,000 time steps [i.e., after the change in the environment of the population with enclaves has had a chance to have an effect and in fact population size is much reduced in the population with enclaves (cf. Figure 1)], what we find is that the individuals living as separate subpopulations in isolated enclaves possess on the average less eating ability than the individuals living as a single population free to move in the entire environment. How can this deterioration in a genetically transmitted ability be explained?

The probability that an individual will eat, and therefore will survive and reproduce, depends not only on the individual's genetically transmitted ability to find food but also on the local availability of food. If one individual lives in a food-poor environment and another individual in a food-rich environment, the first individual will eat less than the second individual even if the first individual is more able to find food than the second individual. Notice, however, that from an evolutionary point of view the two factors that control eating do not have the same meaning. The "ability" factor represents a selective pressure for the evolutionary emergence of higher levels of food-finding ability or at least for the maintenance of current levels. In contrast, the "local availability of food" factor is a chance factor from an evolutionary point of view in that the individuals that eat more (and therefore have more offspring) because they happen to live in a food-rich environment need not have higher levels of food-finding ability. Hence, in so far as the "local availability of food" factor becomes important in determining who reproduces and who does not reproduce, the natural selection process will become less efficient in selecting more able individuals.

We believe that this might explain why there is an evolutionary deterioration in food-finding ability in the population living in separate enclaves. In the population without enclaves an individual that is good at finding food and that happens to find itself in a food-poor local environment can move to another more food-rich environment to survive and reproduce. Hence, its good "genes" will be maintained in the population. In the population with enclaves individuals with good "genes" that find themselves in food-poor enclaves may not reproduce because they cannot leave the enclave, whereas other individuals with less good "genes" may find themselves in food-rich enclaves and reproduce, that is, transmit their "genes," even if their genes are not very good. Hence, there will be less strong selective pressure for food-finding ability and more purely chance reproduction of individuals. The net result is that although the original level of food-finding ability is maintained in the population without enclaves, such level will somewhat deteriorate in the population with enclaves, and this will accelerate the cumulative process of extinction in this population.

That the enclaves are the critical factor, both ecologically and genetically, in determining the eventual extinction of populations living in enclaves is shown by some parametric manipulations of our simulations. In the simulation we have described the environment was divided up into 5 × 5 = 25 enclaves of 20 × 20 = 400 cells each. We have done two other simulations with 2 × 2 = 4 enclaves (50 × 50 = 2,500 cells each) in one case and with 10 × 10 = 100 enclaves (only 10 × 10 = 100 cells each) in the other. As predicted, there is no extinction in the first case, whereas there is a much faster extinction in the second case compared with our main simulation with 25 enclaves. Hence, we conclude that survival depends on the quantity of available space.

Another genetic effect of living in enclaves is on genetic variability and, more specifically, on the number of different lineages still existing at various times during evolution. A lineage is a set of genetically related individuals, all descending from a single ancestor in the initial population. If we count the number of different lineages in the populations with and without enclaves, we find that the population with enclaves includes more different lineages than the population without enclaves up until time step 15,000 and beyond. Evidently, separation between subpopulations keeps in existence lineages that are not particularly good and that would become extinct in a population without enclaves.

THE EVOLUTION OF ARTIFACTS IN POPULATIONS WITH AND WITHOUT ENCLAVES

Imagine now that in addition to extracting energy from nature (food) the individuals in our populations have another resource: technological artifacts. An artifact (e.g., a vase for storing or cooking food) is something created by the organisms that allows the individual using the artifact to increase the amount of energy extracted from food. In our simulations if a single food element is consumed without using artifacts, its energy value for the organism is 10. If food consumption is accompanied by the use of artifacts, the quantity of energy extracted from a single food element is increased, and it can become, say, 15. In other words, artifacts function as multipliers of energy extracted from food. Individual artifacts vary in their physical properties, and the properties possessed by an artifact determine its quality (i.e., how much the particular artifact increases the energy extracted from food). The best artifacts can double the energy extracted from a single food element, that is, 20 energy units. The worst artifacts can be useless, that is, they can leave the energy extracted from food at 10.

When our two populations have reached a steady state in both population size and average level of food-finding ability and a change occurs in the environment of one of the two populations with the appearance of enclaves, another thing happens to both populations. Each individual in the population is given a certain number of artifacts for storing or processing food. Because the artifacts function as multipliers of the energy extracted from the food elements that the individual is able to capture in the environment, the survival/reproductive chances of an individual now depend both on the individual's food-finding ability (and the local availability of food) and on the quality of the artifacts used by the individual. The initial pool of artifacts has randomly generated properties, and therefore, the average quality of the artifacts is not very good and their influence on the selective process operating on the organisms is not very great. However, there is evolution of artifacts much as there is evolution of organisms. When an individual dies, its artifacts disappear with the individual. However, when a new individual is born, the new individual is given a certain number of artifacts selected from the best artifacts of the current artifact pool of the population. These artifacts function as models to be reproduced by the individual, which will then use the copies for storing or processing its food. In the course of the reproduction (copying) process the properties of the reproduced artifacts are slightly changed on a random basis, and therefore the artifacts used by the individual are partly new. As in the case of genetic mutations these new artifacts in most cases turn out to be less good that the models from which they were copied, but in some infrequent cases they are of better quality than the models from which they are derived. The selective reproduction of the best artifacts and the constant addition of random variability to the artifact pool tend to result in an evolutionary increase in the average quality of artifacts [6].

Details of the Simulation

Each artifact has physical properties that are described by 10 binary values. These properties determine the quality of the artifact. One particular randomly chosen string of 10 bits is considered as the best possible artifact. If an individual were to use this best artifact the energy the individual would extract from the food elements captured in the environment would double (20 energy units instead of 10). The quality of each particular artifact is measured as the difference (Hamming distance) between the artifact and the best possible artifact. The worst, that is, most distant, artifact leaves the energy extracted from one food element at a value of 10. The amount of energy extracted by an individual from a single food element captured by the individual is therefore 10 times the average quality of the artifacts used by the individual.

An initial pool of 100 artifacts is created by randomly generating 100 strings of 10 bits. Five of these 100 artifacts, randomly chosen, are assigned to each of the 200 individuals of the population at the moment the artifacts are introduced. Hence, from this point on the energy of each individual depends on both the number of food elements the individual is able to capture and the average quality of the 5 artifacts the individual is using. When a new individual is born, the individual is assigned 5 artifacts as models to be reproduced. These 5 artifacts are randomly selected from among the best artifacts currently used either by the total population or by the subpopulation living in an enclave, according to the simulation. (In Ugolini and Parisi [6] different criteria for selecting the artifacts for reproduction are explored; cf. Boyd and Richerson [7]). These 5 artifacts are used as models to be reproduced by the new individual in the following way. Each individual has a second neural network, in addition to the network controlling the individual's movements in the environment. The connection weights of this second network are randomly generated when the individual is born. The network has 10 input units, 4 hidden units, and 10 output units. The 10 input units encode the properties of the particular model artifact to be reproduced, and the 10 output units encode the properties of the artifact which is produced as a copy. The network learns to produce the copy using the properties of the model artifact as teaching input as part of the backpropagation procedure. In other words, the task the network is learning is an auto-association task: the network learns to generate an output identical to the input. However, some random noise is added to the teaching input in such a way that the artifact copy that is produced is similar but not identical to the model. This allows the production of new artifacts that at least in some cases turn out to be of better quality than the artifacts used as models. Each individual uses the artifact copies it has produced to store or process food.

Results

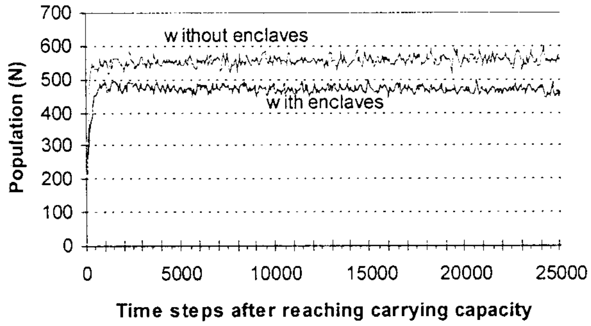
What are the consequences of possessing an evolving pool of artifacts for the population without enclaves and for the population with enclaves? Let us consider the population without enclaves first. Because the artifacts have the effect of increasing the energy extracted from captured food, there will be a tendency for the individuals in this population to have more energy and therefore to live longer and have more offspring. The result is that population size is greater in the population with artifacts compared with the population without artifacts. More individuals can manage to live in a given environment if they possess artifacts that increase the amount of energy extracted from the environment.

The consequences of possessing artifacts are even more significant for the population with enclaves. As we know, in our simulations a population made up of subpopulations living in isolated enclaves tends to become extinct. The addition of artifacts changes this situation. Artifacts increase the amount of energy the organisms extract from the environment and therefore make them more resistant to locally stressful conditions. In fact the results of our simulations are that a population living in enclaves can avoid extinction if the population uses artifacts to increase the energy extracted from food. The critical factor determining the extinction of a subpopulation living in an enclave is the temporary local scarcity of food. Artifacts increase the energy extracted from the little food that is available, and this may be sufficient for the subpopulation to survive until next year (Figure 2).

However, the artifacts appear to be able to counter only one of the two factors that are in operation in an environment subdivided in enclaves and that cause extinction in populations without artifacts: the ecological factor of spatial heterogeneity in food availability. The other factor, that is, genetic deterioration due to a less efficient selective process for the organisms, remains operative even in populations with artifacts. If we measure the food-finding ability of the organisms in the two populations with artifacts, we find that after a certain number of generations the population with enclaves has a lower level of food-finding ability than the population without enclaves.

Genetic deterioration can be one factor that explains why population size is greater in the population without enclaves than in the population with enclaves. Another factor could be artifact quality. Living in enclaves appears to have a negative effect on the evolution of the quality of artifacts. Subpopulations living in isolated enclaves and making copies of the artifacts existing within the enclave,

FIGURE 2



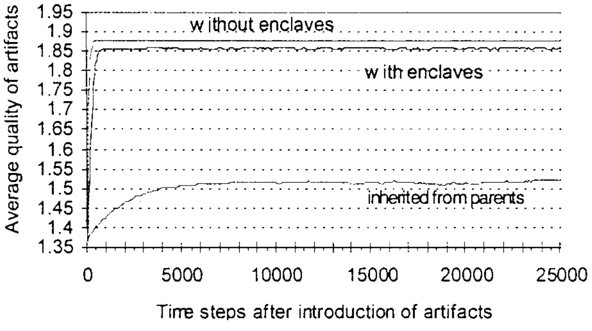
Population size for a population with enclaves and for a population without enclaves, both using artifacts. (Average of six replications.)

without external exchanges and influences, may progressively improve the quality of their artifact pool, but the evolutionary process of artifact improvement is less brilliant than in a population without enclaves. In a population without enclaves the artifact pool from which the artifacts are selected for reproduction is the entire artifact pool of the population. In contrast, in a population living in enclaves an artifact that is given to a newly born individual as a model to be reproduced is selected from among the best artifacts of the local artifact pool. This of course does not guarantee that an artifact selected for reproduction is among the best artifacts of the entire population. It only guarantees that it is among the locally best artifacts. Hence, one can predict that the evolution of artifacts will be less efficient in a population with enclaves than in a population without enclaves and that the artifacts of the former population will be less good than those of the latter population. The results of our simulations show this to be the case. Although the quality of artifacts improves evolutionarily in both populations, the artifacts of the population with enclaves remain of inferior quality than those of the population without enclaves (Figure 3).

However, the selective process has considerable force even in the population living in enclaves. This is shown by a comparison with a third population in which there is no selection of globally or locally best artifacts but an individual inherits the artifacts of its (single) parent (Cavalli-Sforza and Feldmann's [8] vertical transmission; Figure 3).

Another consequence of leaving in enclaves is that enclaves create subcultures of artifacts. If we measure artifact similarity within enclaves and across enclaves, we find that an artifact tends to be more similar to another artifact within the same enclave than to an artifact outside the enclave. Enclaves maintain separate subcultures of artifacts that tend to disappear when there are no enclaves. One could say that enclaves tend to increase the number of existing artifact lineages as they increase the number of existing genetic lineages (see above).

FIGURE 3



Evolution of the quality of artifacts in populations with and without enclaves. Data from a population in which an individual inherits the artifacts of its (single) parent are also shown. (Average of six replications.)

Finally, we briefly mention the results of another set of simulations in which enclaves exist for artifacts but not for individuals. The individuals are free to move in the entire environment, but when a new individual is born (and is placed near the current location of its parent), the artifacts given to the individual as models to be reproduced are selected from the best artifacts of the enclave in which the individual happens to be located and not from the total artifact pool. The results of these simulations show that after an initial period in which population size is higher in the population without enclaves than in this new population with enclaves only for artifacts, in the long run the two population sizes tend to be the same—and higher than in the population with enclaves for both individuals and artifacts. And the same pattern of results is obtained with respect to the quality of artifacts.

DISCUSSION

In the simulations described in this article we have examined some effects of living in isolated environments. If the environment has spatially and temporarlly variable resources (as was the case, e.g., for prehistoric American Southwest [9]), being confined to an enclave can lead to the extinction of the local population because the local population cannot react to the temporary scarcity of resources by moving to a different environment with more resources. Cumulative local extinctions then lead to the extinction of the entire population. Another effect of being confined to a local environment with considerable resource variability is that the selective pressures for better genes are weakened in that individuals may reproduce because they happen to be in resource-rich local environments and not because they have better genes. Hence, populations living in isolated environments may have fewer good genes and lower levels of ability than populations that can move from one to another portion of the environment in search of local environments with more resources. Displacements in the environment can make an objectively heterogeneous environment more homogeneous from the point of view of the organisms in that the organisms can constantly live in local environments with sufficient resources if they can move from local environments temporarily (or permanently) empty of resources to other environments with more resources. On the other hand, if it is impossible for whatever reasons to leave the local environment (the enclave) spatial/temporal heterogeneity in resource availability leads to local extinctions that by accumulating over time may cause the total extinction of the population.

Another effect of living in enclaves concerns the evolution of technology. Although artifacts can allow a population living in enclaves to survive, our simulations show that artifacts reach a lower level of quality evolutionarily and total population size is smaller if the artifact pool from which the best artifacts are selected for reproduction is restricted to the enclave. Selecting from among the locally best artifacts rather than from the globally best artifacts (i.e., from artifacts outside one's enclave) tends to have a depressing effect on the evolution of artifacts. Furthermore, in our simulations we consider only one mechanism that adds new variability to the artifact pool, that is, random changes occurring in the copied artifact with respect to the artifact taken as model (analogous to random mutations in biological evolution). However, if another source of new variants is incorporated in the simulations, i.e., new artifacts that represent new combinations of properties of various existing artifacts (analogous to sexual recombination in biological evolution), then living in an enclave would have further negative effects on technological evolution. The inability to consider artifacts outside one's own enclave as potential sources of inspiration for new artifacts would restrict artifact variability and therefore would further depress artifact evolution.

As we have suggested, enclaves defined as local environments that cannot be left by the population living in the enclave and cannot be penetrated by artifacts and ideas from outside can result from a variety of factors. Beyond geographical and political-cultural isolation, a third cause can be "circumscription" [10], that is, more or less hostile peoples living nearby that make it impossible to expand outside one's boundaries. Because living in an enclave has various negative consequences, it is to be expected that local populations will tend to develop ways to get over the "walls" of their enclave and to expand beyond it. This expansion can take various forms. One is territorial expansion. Another is exchange of resources with populations outside one's territory. A third is copying artifacts and culturally transmitted behaviors and ideas of other people and exporting one's artifacts and behaviors as models to be copied [11].

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