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Case 4:
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- cooperation is maintained most effectively when there is assortment (correlated interactions) among types. When cooperators interact with cooperators, there is an opportunity for individual-level costs to be traded against the benefit that accrues at the collective level.
- In spatially structured environments, cooperating types interact with like more often than by random encounters with other members of the population. Moreover, interacting individuals of the same type often are genetically related.
- Spatial structure is especially relevant to the establishment of the earliest kinds of collectives and is exemplified in experimental studies with the bacterium Pseudomonas fluorescens where in spatially structured microcosms cooperation evolves de novo (from asocial ancestral types) (Rainey & Rainey 2003) via mutations that result in overproduction of adhesive glues
- Although spatial structure can tip the balance in favor of cooperating types, it also intensifies competition among cooperating types, which may reduce selection for cooperation
- This establishes conditions likely to lead to conflict (Hurst et al. 1996), unless particular mechanisms evolve: for example, mechanisms that foster restraint among cooperating types, mechanisms of self-policing that punish selfish types.
- mechanisms that randomize group members such that each has equal chance of accessing limited resources
- In the context of primordial collectives, mechanisms that promote the mixing of cooperating types within clusters may be important in reducing opportunities for defection. An additional factor is population size: If competition is among few individuals, then collective-level benefits arising from more efficient resource utilization can be returned to individuals without compromising collective benefit (Pfeiffer & Bonhoeffer 2002). From a game-theoretical perspective, this corresponds to the fact that cooperation affirms with greater ease in small groups where direct benefits are achievable
- Any mechanism that generates higher genetic relatedness will enhance the evolution of higher levels of cooperation whenever collective behavior is genetically determined (Gardner & Grafen 2009). However, cooperating types do not need to be genetically identical. Rather, advantages accruing from participation in collective (cooperative) behavior must simply deliver fitness benefits for those with a tendency to transmit such behavior to their offspring.
- The most effective of this class of genes are referred to as green-beard genes. These genes encode behaviors that cause cooperators to associate with each other (Dawkins 1976, Gardner & West 2010). Although green-beard genes are susceptible to cheating, they are not uncommon in nature (see Gardner & West 2010). One example is the cell adhesion gene csa found in cellular slime mold: When expressed, it causes carriers to adhere, aggregate, and form cooperative fruiting bodies. Cells not expressing csa are excluded from social groups (Queller et al. 2003). One interesting aspect of green-beard genes is their capacity to favor cooperative behavior by causing direct harm to types (potentially defectors) that do not express the green-beard gene, as in the abovementioned colicin-producing bacteria. Perhaps in the activities, dynamics, and evolution of green-beard genes, particularly among single-celled organisms, lie the foundations of self-recognition, self-policing, and punishment systems that manifest as important components of complex multicellular life
- Well-recognized mechanisms include developmental programs that control cell growth and limit, through apoptosis, opportunities for unchecked proliferation as well as the capacity to distinguish self from other and to effect punishment against rogue types. Also of importance for minimizing conflict is reproduction via a single-cell bottleneck and germline sequestration.
- d, the conflict between the reproductive success of the two levels can be overcome by the presence of a trade-off between fecundity and viability, which allows selection at the higher level to influence life-history traits