Synopsis

Cooperation is ubiquitous across taxa in the animal kingdom. For example, microbes cooperate in producing antibiotic-resistant biofilms, mammals and birds collectively mob predators, and humans cooperate in utilization of common resources. Sometimes, cooperation is costly. Such behaviours lead to a paradox: why does natural selection favour a costly behaviour? In a well-mixed population, cooperators are susceptible to be invaded by defectors. The evolution and maintenance of cooperators requires structured populations. One of the key mechanisms that can promote cooperation is a spatial structure with local clustering of cooperators (and defectors). This exposes defectors to the consequences of their own selfish behaviour, keeping them in check. However, a vast fraction of cooperative species is mobile. Movement allows defectors to escape their fate, destroying spatial structure and hindering cooperation. Therefore, cooperation is typically thought to be difficult to evolve in mobile organisms. In this thesis, we question this assumption, and using simulation and analytical studies, show that coevolutionary dynamics can promote cooperation in mobile populations.

Species across taxa, ranging from cells and microbes to fish, birds and ungulates, live in highly mobile groups that frequently merge and split, called fission-fusion groups. Fission-fusion dynamics typically causes mixing of the population. Therefore, cooperation is not considered viable in such groups. The macroscopic dynamics of these groups is governed by local cohesive interactions between individuals. In Chapter 2, using explicit spatial agent-based evolutionary simulations, we explore the coevolution of cooperation and local cohesive tendencies as a possible route to cooperation in such populations. Studies on collective behaviour have previously shown that individuals can self-sort based on traits such as speed or cohesion. However, these insights have not been applied to study cooperation. We use the ideas of assortment (where cooperators interact more frequently with other cooperators) and multilevel selection (where selection for cooperation between groups outweighs selection against them within groups) to understand the coevolutionary dynamics. We discover an interplay among cooperation and grouping, where self-assorted groups favour cooperation, and cooperative interactions in turn favour such groups. As a result of these dynamics, we find an oscillatory pattern of cooperation and defection caused by an arms race for the costly cohesive trait. This maintains cooperation even in the absence of well known mechanisms such as kin interactions, reciprocity, local dispersal or conditional strategies that require information on others' strategies or payoffs. Our results reveal the possibility of cooperative aggregations in dynamic fission-fusion populations. Our study reveals simple conditions under which greenbeard cooperation can evolve via an arms race for the costly greenbeard trait.

In Chapter 3, we generalize our coevolutionary model to any generic greenbeard coop-

eration, by considering a coevolving phenotypic trait (the greenbeard) that mediates cooperative interactions. Greenbeard cooperation is viable only if the cooperative gene is linked to the greenbeard gene. It is typically thought to be unstable over time, because defectors who evolve the greenbeard can invade cooperators. In Chapter 3, we explore whether coevolutionary dynamics can help stabilize greenbeard cooperation. Evolution happens via two key processes: selection and drift. Unlike typical models of evolution that often employ only one of these, we develop an analytical model that combines both. Our model employs techniques from statistical physics to derive coupled Chemical Langevin Equations for a finite population of organisms. By accounting for the costs of the greenbeard, we demonstrate that a combination of selection, mutations and demographic noise in a structured population can lead to spontaneous emergence of linkage between the cooperative and greenbeard genes. We find a cyclical dynamics with a decay and re-emergence of the greenbeard. On average, we find significant levels of both cooperation and the greenbeard, including fixation of both traits under some conditions.

Positive assortment of cooperators is the general condition for cooperation to evolve. However, assormtent is theoretically zero in infinite well-mixed populations. Real populations may deviate from this theoretical ideal due to finite population size, and due to presence of smaller interacting subgroups within the population. Variation in the group sizes and compositions may occasionally lead to assortment, just by chance. Furthermore, the presence of solitary individuls critically affects assortment. Yet, in our knowledge, no studies have quantitatively characterized assortment in group-structured finite populations. In Chapter 4, we characterize assortment arising from such a random group structure in finite populations. We find that the variance in assortment is inversely proportional to population size and interacting group size. We also show that if grouping is random, assortment decreases linearly with the proportion of solitary individuals. Our result may be helpful in establishing a null model for assortment in empirical studies on spatial structure. Furthermore, our results reveal that stochasticity in assortment effectively leads to an increase in drift, which could maintain higher levels of cooperation than in well populations.

In Chapter 5, we allow mobility itself to coevolve with cooperation, in a human context. Humans cooperate in the utilization of spatial ecological public goods, such as forest produce, fisheries, and grazing lands. However, humans evolve their strategies via social learning, by imitating more successful individuals. Here, apart from mobility, space introduces the possibility of incomplete information availability. Further, dynamics of the renewable resource may evoke eco-evolutionary feedbacks. Very few studies on cooperation have explored the coevolution of cooperation and costly dispersal, and fewer still explicitly account for a renewable resource. No study to our knowledge has considered the effects of spatial information access. Here, we integrate all three features into a minimal, agent-based, evolutionary model to study human harvesting and dispersal strategies. We show that, as resource utility increases and dispersal becomes cheaper, societies progress from a sedentary, subsistence-oriented lifestyle, through a nomadic phase characterized by efficient and equitable resource harvest, to eventual social stratification and overexploitation of the resource. Further, impatience and myopia among consumers tend to promote cheater strategies, leading to unequal and inefficient harvest. Our model provides insights into the harvesting and dispersal strategies of hunter-gatherers, nomadic pastoralists and shifting cultivators across the world, throughout human history.

In conclusion, we investigated coevolutionary dynamics across a spectrum of mobility, from highly mobile to almost sedentary populations. We found that when the second trait (cohesion, greenbeard, or dispersal) is costly, coevolutionary dynamics can facilitate the evolution of cooperation in cases where it was previously not considered viable. In fact, cooperation does not sustain if the other trait is not costly. In the process, we also obtained insights into the role of other factors, such as demographic stochasticity, rapid evolution, incomplete information and eco-evolutionary feedbacks, on spatial evolutionary dynamics.