THÈSE

PRÉSENTÉE À

L'UNIVERSITÉ PIERRE ET MARIE CURIE

École doctorale Informatique, Télécommunications et Électronique (Paris) (ED130)

Présentée par **Thomas GARCIA**

pour obtenir le grade de **DOCTEUR**

DÉTERMINANTS ÉVOLUTIONNISTES DE LA SOCIALITÉ :

LE RÔLE DE LA FORMATION DE GROUPE

Directeur de recherche : Édith PERRIER

Co-directeurs de recherche : Silvia DE MONTE et Leonardo GREGORY BRUNNET

Soutenance le 4 décembre 2013 à l'École Normale Supérieure (Paris) devant la commission d'examen formée de :

Pr. Bernard CAZELLES	UMR 7625 CNRS, Laboratoire Écologie et Évolution, ENS, Paris	Président du jury
Pr. Paul RAINEY	NZ Institute for Advance Study, Massey University, Auckland	Rapporteur
Pr. Guillaume BESLON	UMR 5205 CNRS, Institut National des Sciences Appliquées, Lyon	Rapporteur
Dr. Minus VAN BAALEN	UMR 7625 CNRS, Laboratoire Écologie et Évolution, ENS, Paris	Examinateur
Pr. Michael DOEBELI	Department of Zoology, University of British Columbia, Vancouver	Examinateur
Dr. Clément NIZAK	UMR 5588, Laboratoire Interdisciplinaire de Physique, Saint Martin d'Hères	Examinateur
DR Édith PERRIER	UMI UMMISCO, Centre IRD Île-de-France, Bondy	Dir. de thèse
Dr. Silvia DE MONTE	UMR 7625 CNRS, Laboratoire Écologie et Évolution, ENS, Paris	Dir. de thèse

Remerciements

Je tiens d'abord à remercier Silvia, qui a été mon interlocutrice principale pendant ces trois ans et qui s’est toujours montrée disponible malgré un emploi du temps chargé. Elle a su orienter ma recherche dans la bonne direction en me détournant de mes (((bien) trop) nombreuses) digressions sans les censurer et en me laissant une marge de liberté considérable. C’est pour moi un attrait décisif de la recherche, et je lui suis reconnaissant d’avoir su le respecter. Grazie !

Leonardo, qui m’a gentiment accueilli dans son labo de Porto Alegre, et hébergé dans sa famille pendant un mois. Le reste du temps, il a été l’interlocuteur idéal pour comprendre le comportement parfois capricieux de mes particules bleues et rouges. Obrigado, je n’oublierai pas les foisonnants barbecues et les délicieux vins chiliens.

Enfin, je remercie Edith pour son soutien constant dans mes démarches et ses conseils avisés, ainsi que l’équipe du PDI-MSC et ses étudiants des quatre coins du monde.

Je voudrais au moins mentionner également, en vrac :

les collègues de l’équipe Ecologie et évolution ; les thésard-e-s croisé-e-s à Dresde et Göttingen, avec qui j'ai partagé aussi bien des discussions techniques que des Lagavulin, et celles et ceux qui ont fait de l’institut de physique de l’université de Porto Alegre une terre accueillante pour un non-lusophone ; Guilhem et Orso, brillants collègues de fin de thèse ; Antoine et Joseph, compagnons de pauses café-madeleines, pour les discussions scientifiques et politiques ; mes autres ami-e-s et collègues parisiens avec qui j’ai pu discuter de tout, tant qu’il ne s’agit pas de la thèse !

Enfin un grand merci à ma famille pour m’avoir sorti la tête de mes modèles à l’occasion de repas toujours gargantuesques, ainsi qu’à Canelle et Chlamy-von-Dindon (glou glou !) pour les séquences grattouilles.

Et surtout, ma mère, qui s’est pliée en quatre pour que j’en sois là aujourd’hui et m’a toujours épaulé, et Margot, soutien indéfectible malgré mes doutes et sautes d’humeur. Sans vous ces cent-je-ne-sais-combien pages n’auraient été rédigées. Merci pour tout.

Contents

1 Evolutionary game theory for the evolution of cooperation in microbes 1
1.1 The intimidating field of social evolution . . . 2
1.1.1 Sociality/cooperation is puzzling for the evolutionary biologist . . . 2
1.1.2 A scientific shift in the current approach . . . 3
1.2 Sociality and cooperation in microbes . . . 4
1.2.1 Microorganisms are good systems to test evolutionary hypotheses . . . 4
1.2.2 Sociality and cooperation are pervasive in microbes . . . 5
1.2.3 The tragedy of the commons in microbes . . . 6
1.2.4 The chicken-and-egg of cooperation and sociality . . . 8
1.3 Solving the paradox of cooperation . . . 9
1.3.1 Reciprocity . . . 9
1.3.2 Policing (reward / punishment) . . . 10
1.3.3 Interactions directed toward genealogical kin . . . 11
1.3.4 Assortment between cooperators . . . 12
1.3.5 Direct benefits . . . 13
1.3.6 Game definition . . . 14
1.4 Game structure . . . 14
1.4.1 Dyadic games . . . 15
1.4.2 N-player games . . . 17
1.4.3 The difficulty finding the right game . . . 22
1.5 Population structure . . . 25
1.5.1 Lattices . . . 25
1.5.2 Graphs . . . 27
1.5.3 Continuous space . . . 28
1.6 Group structure . . . 29
1.6.1 Groups as equivalence classes . . . 29
1.6.2 Groups as sets . . . 29
1.6.3 Non-delimited groups . . . 30
1.7 Outline . . . 31

2 Group formation and the evolution of sociality 35
2.1 Introduction . . . 35
2.2 General formulation . . . 39

- 2.2.1 Hypotheses . . . 39
- 2.2.2 Payoff difference for a general aggregation process . . . 41
- 2.2.3 Payoff difference: case of no assortment *a priori* . . . 43
- 2.3 Group formation by differential attachment . . . 46
  - 2.3.1 Description of the toy model . . . 46
  - 2.3.2 Group size distributions and payoff difference . . . 49
  - 2.3.3 Evolutionary dynamics and effect of the parameters . . . 49
  - 2.3.4 Other rules for group formation . . . 54
- 2.4 Decoupling cooperation and attachment . . . 55
  - 2.4.1 Hypotheses . . . 55
  - 2.4.2 Evolutionary outcome . . . 57
  - 2.4.3 Conclusion . . . 60
- 2.5 Extension to a continuous trait . . . 61
  - 2.5.1 Changes in the model . . . 61
  - 2.5.2 Resident / mutant analysis . . . 64
  - 2.5.3 Application to an aggregation process . . . 67
  - 2.5.4 Condition for altruism . . . 68
- 2.6 Discussion . . . 70
  - 2.6.1 Social groups formation and evolution . . . 70
  - 2.6.2 Aggregative sociality in microorganisms . . . 73
  - 2.6.3 Nonnepotistic greenbeards? . . . 74
  - 2.6.4 About altruism and direct benefits . . . 75
  - 2.6.5 Toward a re-evaluation of the group formation step . . . 77

3 Differential adhesion between moving particles for the evolution of social groups 79
- 3.1 Introduction . . . 79
  - 3.1.1 Main issue . . . 79
  - 3.1.2 Outline . . . 81
- 3.2 Model . . . 82
  - 3.2.1 Aggregation model . . . 83
  - 3.2.2 Social dilemma . . . 86
  - 3.2.3 Evolutionary algorithm . . . 90
- 3.3 Results . . . 91
  - 3.3.1 Local differences in adhesion rule group formation and spatial assortment in the aggregation phase . . . 91
  - 3.3.2 Assortment and differential volatility between strategies drive the evolution of sociality . . . 93
  - 3.3.3 Parameters of motion and interaction condition the evolution of sociality 97
- 3.4 Discussion . . . 105
  - 3.4.1 Evolution of sociality via differential adhesion . . . 105
  - 3.4.2 Strategy assortment and differential volatility . . . 105
  - 3.4.3 Role of group formation . . . 107
  - 3.4.4 Conclusion . . . 108

3.5 Effect of ecological vs. evolutionary time scale 109
    3.5.1 Hypotheses 109
    3.5.2 Evolutionary trajectories 110
    3.5.3 Effect of the generation time 113
    3.5.4 Conclusion: role of time scales 116

4 Conclusion **119**
4.1 Main results 119
4.2 Perspectives for future work 128

Appendix A Derivation of the payoff difference, general case **145**

Appendix B Group size distributions for differential attachment **151**

Appendix C Condition for sociality to be altruistic for differential attachment **155**

Appendix D Evolutionary algorithm for chapter 3 **157**

List of Figures

1.1 A Venn diagram for cooperation and sociality 8
1.2 Representation of the Prisoner's Dilemma, the Snowdrift Game, the Stag Hunt and the Harmony Game in the (T, S) plane. 17
1.3 Payoff difference between cooperators and defectors in a threshold game. 22
1.4 Payoff difference between cooperators and defectors in a threshold game when N varies. 23

2.1 Life cycle used in the model 40
2.2 Payoff difference changing one parameter at a time 50
2.3 Evolutionary trajectory and group size dynamics 51
2.4 Social invasion thresholds 52
2.5 Mean fitnesses of the **S** and **A** strategies when **S**s invade from scratch in a small population ($N_{pop} = 1000$) 53
2.6 Payoff differences for other rules of attachment 56
2.7 Equilibrium frequencies of each strategy **SC**, **SD**, **AC**, **AD** when sociality is decoupled from cooperation. 58
2.8 A non-generic case of evolutionary trajectories in the 3D-simplex for various initial conditions. 60
2.9 Pairwise invasibility plots (PIP) 64
2.10 Analytical and computational pairwise invasibility plots for the continuous model 68
2.11 Sensitivity of the pairwise invasibility plot on parameters b/c and T 69
2.12 The Simpson's paradox 72
2.13 Minimal b/c ratio to promote sociality vs. maximal b/c ratio for sociality to be altruistic. 76

3.1 Local rules for interaction 85
3.2 Segmentation of a structured population into groups 88
3.3 Snapshots of an aggregation process 93
3.4 Evolutionary dynamics 95
3.5 Effect of motion noise on u_S, u_A, R_S and R_A and on the evolutionary equilibria . 99
3.6 Effect of velocity on u_S, u_A, R_S and R_A and on the evolutionary equilibria 101
3.7 Effect of the interaction radius on u_S, u_A, R_S and R_A and on the evolutionary equilibria 103
3.8 Effect of density on the evolutionary equilibria 104

3.9 Snapshots of an evolutionary trajectory with motion and reproduction concomitant: case when **S**s dominate 111
3.10 Snapshots of an evolutionary trajectory with motion and reproduction concomitant: case when **A**s dominate 112
3.11 Example of bistable equilibrium when the evolutionary and ecological time scales are no longer separated. 114
3.12 Effect of the generation time t_R on the average equilibrium frequency of **S** players. 115
3.13 Evolutionary fate of the cooperative trait in Cremer et al.'s model, as a function of regrouping time T 116

4.1 Effect of the group size distribution on the maximal benefit-to-cost ratio for altruism 122
4.2 Invasion barrier required to trigger sociality, as a function of the patch size T. . . 124
4.3 Formation of groups in *Dictyostelium discoideum* and in cadherin-expressing L cells 127
4.4 Spatial cell sorting in *S. cerevisiae* and in cadherin-expressing L cells 128

B.1 Theoretical group size distributions for social and asocial individuals. 153

Chapter 1

Evolutionary game theory for the evolution of cooperation in microbes

Foreword

The following work pertains to the sub-discipline of evolutionary biology coined “the evolution of cooperation” and widely borrows from its formalism, lexicon and, possibly, shortcomings. Hopefully, it will manage to question some of its presuppositions at the same time. While this introduction chapter provides a – short – overview on the – extensive – literature on cooperation theory, it does certainly not claim exhaustiveness. Rather, it is intended to give the minimal context necessary to understand the stakes of the thesis, and supply readers with a methodological toolbox. In three years, my understanding of this research field has been constantly shaped by going back and forth through some of its numerous sides, and primarily guided by my own interests at a given point in time. As a consequence, my goal is to paint here my own, idiosyncratic vision of the landscape of sociobology, and give clues on how I hobbled along through the paths of theoretical evolutionary biology to end up writing this. Some details will be eventually re-discussed in the following chapters, but I think they will be best kept in mind if hinted at beforehand.

A lexical word of caution: the terms *sociality* and *cooperation* will be used indifferently in the few first sections. However, it is actually one of my main points to stress a distinction between the two, and to underline what implications the confusion between these two concepts might have had on the methodology employed in theoretical / conceptual models.

The main framework is evolutionary modeling; the main issue is living in groups; the main question is “how?”; the main focus, on microorganisms. So let us start.

1.1 The intimidating field of social evolution

1.1.1 Sociality/cooperation is puzzling for the evolutionary biologist

With more than half a century of controversies, semantic issues and rises and falls of its successive towering paradigms, the field of social evolution might not be the most friendly one. While undeniable progress has been made, decades of field and lab work, abstract models and epistemological questioning have not succeeded in establishing a consensual theory to describe and rank the main driving forces behind the emergence and sustainability of sociality in the living world. How is collective structuring of populations conceivable in a Darwinian – thus intrinsically competitive – world ? The issue is still puzzling considering the ubiquity of social behavior at all levels of biological organization. Charles Darwin himself identified it as a potential weak spot in his theory when he described sociality in ants as “one special difficulty, which at first appeared to [himself] insuperable, and actually fatal to [his own] theory” (Darwin, 1871). The question of the origin and sustainability of social traits has been revived in the last decades following Hamilton’s breakthrough paper on kin selection (Hamilton, 1964) and Maynard Smith’s identification of multicellularity and eusociality as ones of life’s major transitions (Maynard-Smith and Szathmáry, 1995). Since then, this issue has spawned a plethoric literature (Sumpter,

2010) that reaches fields as diverse as ethology, theoretical ecology, microbiology, anthropology, sociology (or rather, a new portmanteau word, "sociobiology"), mathematics, economics, statistical physics, etc.

Disclaimer: in some circumstances, biologists might have the tendency to overestimate the scope of their perception of the mechanisms behind sociality. The point of view of the evolutionary biologist should not however obfuscate the work of researchers in humanities, and certainly the issues we tackle as biologists are not the alpha and omega on social theory.

1.1.2 A scientific shift in the current approach

The history of evolutionary biology is tempestuous. I will not try to trace it back; refer to Kutschera and Niklas (2004) for a global overview. While efforts have been made to assemble the disparate works and conceptions into an harmonized global theory (a.k.a. the "Modern Synthesis"), controversies abound and dogmas clash; in the field of social evolution, perhaps more than elsewhere (see the recent dispute on the generality or not of kin selection launched by Nowak 2010's article on Nature (Nowak et al., 2010a)).

Inherited from Darwin, evolutionary biology has kept an ethologist bias. For decades, works on the evolution of cooperation/sociality have mainly focused on large animals, and theoretical works have been motivated by observational studies (Maynard-Smith and Price, 1973; Maynard-Smith, 1982). Examples include social Hymenoptera, e.g. ants and honeybees (Ratnieks et al., 2006; Nowak et al., 2010a) and mammals (most notably, primates (Kappeler and van Schaik, 2002) among which, of course, humans (Melis and Semmann, 2010)). Recent progress in microbiology techniques allows to re-examine in a brand new light the generality and the relevance of the theorems of evolutionary biology on cooperation. The rich social life evidenced in microbes raises new questions and might put in perspective some of its presuppositions.

1.2 Sociality and cooperation in microbes

(The aim of this section is to make readers convinced that microorganisms might hold new keys on the enigma of sociality.)

1.2.1 Microorganisms are good systems to test evolutionary hypotheses

In recent years, the number of studies focusing explicitely on non-intuitive collective behaviors in microbes has dramatically increased, to such extent that species such as *D. discoideum*, *M. xanthus*, *P. aeruginosa* and others have become “superstars” in evolutionary circles (Buckling et al., 2009). There are several good reasons for that. Typically, microorganisms have short generation times and can be monitored *in vitro* in the lab, which allows to follow entire evolutionary trajectories, something that is difficult with larger, slowly reproducing organisms. Moreover, the genomes of several famous species being well documented, they can be easily genetically manipulated and engineered to test various evolutionary scenarii. Experimental biologists can now easily knock out wild-type cooperative genes in social microbes to create cheater mutants and assess the conditions of their failure or success. Importantly enough, microbes amount to a large percentage of life on Earth and no account of sociality is complete were it not validated on smaller organisms. Finally, one of the fundamental questions related to the evolution of sociality is the origin of multicellularity: crudely, how free-living cells form organisms composed of many cells, that can stand on their own? This is a hot scientific issue (Michod and Roze, 2001; Wolpert and Szathmáry, 2002; Sachs, 2008; Rainey and Kerr, 2010; Ratcliff et al., 2012) that combines several sub-questions (the differentiation and division of labor between somatic and germinal cells, the transfer of fitness from the individual to the aggregate, so that the latter become the unit of selection, etc.) Even though the branching of multicellular organisms is deep in the phylogenetic tree, and extant organisms are only exceptionally capable of facultative multicellular states, studying microorganisms that alternate unicellular and multicellular phases may help decipher the origin of multicellularity.

1.2.2 Sociality and cooperation are pervasive in microbes

Microorganisms display a great variety of social behaviors (Crespi, 2001; Velicer, 2003; West et al., 2007a; Nanjundiah and Sathe, 2011; Celiker and Gore, 2013). Here are some examples among the most studied species:

Dictyostelium discoideum is a social amoeba mostly living in a unicellular state that feeds on bacteria. When food is lacking in their environment, cells have the ability to emit a molecular signal (cAMP) that is relayed by their neighbors. Cells follow cAMP gradients until they gather in structured multicellular aggregates that end up forming a mobile slug guided by phototaxis. The slug then morphs into a fruiting body whose stalk is composed of cells that sacrifice to let other cells (spores) at the top be dispersed and colonize new environments (Jiang et al., 1998; Ponte et al., 1998; Li and Purugganan, 2011; Strassmann and Queller, 2011). Similar multicellular stages, where cells undergo differentiation as in metazoans, are found as well in other dyctiostelids, even though aggregation mechanisms differ among species.

Myxococcus xanthus is a bacterium that displays a comparable fruiting body life cycle. *M. xanthus* participates in other kinds of cooperative endeavors as well, e.g. collective swarming (aggregates form by adhesion of extracellular pili at the cell surface and move cohesively owing to a complex motility system; Shimkets (1986a); Velicer and Yu (2003)) or collective predation (cells secrete enzymes that makes prey digestion possible outside the membrane, thus exploitable by potential cheats).

Saccharomyces cerevisiae (a.k.a. budding yeast) can break sucrose into glucose and fructose by externally secreting an enzyme called invertase. The local concentration of invertase in the medium thus acts as a public goods that might be used by nonproducers. Wild-type yeast also tends to bind together and form aggregates (flocculate) that provides them with better protection from chemical stresses (Smukalla et al., 2008). Multicellular states can also be the outcome of directed evolutionary experiments (Ratcliff et al., 2012).

Pseudomonas aeruginosa produces iron-scavenging siderophores that enable cells to transform the environmentally available iron into a form they can feed on. Once emitted outside the cellular membrane, siderophores benefit to any cell in the neighborhood – even potential cheaters – and are as such tantamount to a "common good" (Griffin et al., 2004). Evolutionary experiments evidenced the conflicting propensity to sociality and vulnerability to cheats in *Pseudomonas fluorescens* that socialize by over-secreting adhesive polymers (Rainey and Rainey, 2003).

Other noteworthy examples include biofilms, that provides enhanced protection from predation: the extracellular polymeric matrices that hold the films together are made of substances secreted at the individual level (Nadell et al., 2009); the secretion of virulence factors, antibiotics, exopolysaccharides, signaling molecules used in quorum-sensing, etc.

These examples concur to illustrate that numerous forms of cooperation and sociality are observable in the microbial world. However, they do not all display the same level of elaboration and possibly do not all pertain to the same step in the evolutionary path toward collective structuring. One must indeed distinguish between acts of cooperation that help neighbors or interaction partners in established population and interaction structures, and the very first behaviors that onset those population and interaction structures (Rainey, 2007; Szathmáry, 2011). Interestingly, while many studies focus on the mechanisms supporting the maintenance of the former sophisticated forms of helping traits, far less address the latter. An evolutionary account of the origin of grouping traits is still needed to understand the whole process of microbial sociality.

1.2.3 The tragedy of the commons in microbes

Microorganisms socialize/cooperate *in vivo*. These behaviors are typically costly: they involve metabolic costs (e.g. to produce enzymes) or even the death of the cell, e.g. in the case of fruiting bodies (Nedelcu et al., 2011). *In vitro* experiments show that cooperation, while beneficial for the community (WT cooperating-only populations grow faster than mutant cheating-only populations) is generally costly (in chimeric populations of cooperators + cheaters, cheaters perform better) (Rainey and Rainey, 2003; Gore et al., 2009). Thus cooperation is a trait likely to be exploited by non-cooperators that benefit from the cooperation of others while not paying its cost. Through Darwinian lenses, collective welfare is then expected to collapse, and cooperators to go extinct. This seemingly paradoxical stability of social populations despite what is often referred to as a "tragedy of the commons" (Hardin, 1968; Rankin et al., 2007) is the main puzzle of sociality for the evolutionist.

Box 1.1. A brief lexicon on sociality and cooperation

cooperation: a behavior that benefits to one or several recipient(s), and has evolved for this effect.

altruism: a behavior that benefits to one or several recipient(s) and entails a net cost for the actor. Altruistic acts are a subset of cooperative acts, and are way more challenging to explain.

directly beneficial behavior (or mutualistic cooperation): a behavior that benefits to one or several recipient(s) but profits to the actor as well.

spite: a behavior that imposes a cost on one or several recipient(s) (often at a cost to the actor itself)

sociality: most often, "social" traits are equated to "cooperative" traits in the literature. This leads to the confusion that explaining some forms of cooperation is equivalent to explaining social behavior as a whole. Here, we rather term "social" any trait that enhances the ability of an individual to interact. Sociality could thus refer to a trait that does not provide any benefit to others, i.e. non-cooperative (see Fig. 1.1) In this thesis however, I will focus on social traits that increase individual attachment to a group and enhance group success (e.g. group cohesion), thus also cooperative (see chaps. 2 and 3). Sociality is sometimes referred to as "grouping" (e.g. in Avilés (2002), except that in our work it is costly, hence more challenging to account for).

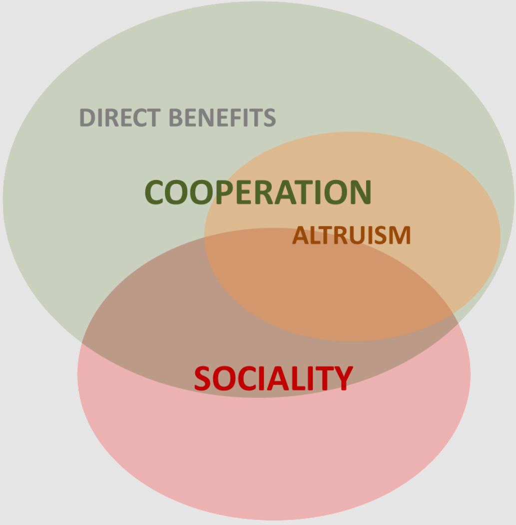

Figure 1.1: A Venn diagram for cooperation and sociality

Cooperation refers to any trait that provides a benefit to one or several recipient(s): it can be either directly beneficial (meaning that the cooperator gets a benefit from its own cooperation too) or altruistic (meaning that the cooperator undergoes a net fitness cost from its cooperation). We call sociality any trait that enhances its carrier's ability to interact. In some cases sociality can be cooperative, when enhanced grouping increases group gains and benefits to each group member irrespective of its social type.

1.2.4 The chicken-and-egg of cooperation and sociality

The purely "social" (in terms of "sticking together" / forming physical groups, e.g. biofilms, yeast flocs, etc.) traits are often mashed with cooperative traits (e.g. contributing to a public good once cells are already living in collectives). In this work, I argue that genes entailing adhesion / attachment may themselves be interpreted as cooperative genes with "something more": an increased ability to have interactions with others (blindly with respect to their social types). See Box 1.1. for a distinction between sociality and cooperation: we mean by "cooperative" any trait that provides a benefit to a recipient, and by "social" any trait that enhances an individual's tendency to interact. In this thesis, we focus on traits that enhance individual's grouping and group cohesion as well (think for instance of a costly glue that makes individuals adhere together) which are at the same time social and cooperative.

1.3 Solving the paradox of cooperation

Game theory is the mathematical framework to address decision-making in rational agents able to adopt several strategies in situations of conflicting interests. In the last few decades, it has been extended to evolutionary biology to describe competition between genetically encoded behaviors. Individuals garner benefits and costs from their interactions, and the frequency of each trait in the population changes in time with natural selection acting the same way as rational choice of strategies: if a trait codes for a behavior that benefits its carrier (in terms of relative reproductive fitness), it will increase in frequency in the population. Here, we review the main mechanisms suggested in the framework of evolutionary game theory to account for the persistence of paradoxical cooperative traits. Numerours attempts to systematize models and classify mechanisms have been made (e.g. by Lehmann and Keller (2006); Nowak (2006); West et al. (2007b)), that bear the ideological standpoints of their authors.

1.3.1 Reciprocity

Modeled on the idea that we humans tend to be more prone to help someone if she has helped us before, Trivers (1971) suggested *direct reciprocation* as a driving mechanism for cooperation in humans, encapsulated by the cathphrase “If you scratch my back, I’ll scratch yours”. In other words: if A helps B, then B helps A. Tit-for-tat strategy was found by Axelrod (1984) to be more successful than most complex strategies in competitions between humans playing the Iterated Prisoner’s Dilemma, but how it applies to animal communities and *a fortiori* microbes is much less straightforward. Indeed, reciprocation strategies require that interactions are repeated with the same player, and that the individual is able to recognize her interaction partner, memorize what she did at the previous timestep and react to the outcome of its last encounter. As a consequence, it remains a very unlikely way toward collective cooperation in microbial species.

Even more cognitively demanding is *indirect (reputation-based) reciprocation* (Nowak and

Sigmund, 1998), that can be summed up as “If I’m seen scratching your back, people will scratch mine”: C sees A helping B, then C helps A. Indirect reciprocity thus requires that interactions are conspicuous and that others are able to monitor and memorize what everyone did in the previous time steps.

A last form coined *generalized reciprocity*, that relies on lighter constraints, was modeled by Pfeiffer et al. (2005): “If someone scratch my back, I’ll scratch the next one”: B is helped by A, B helps C. Individuals base their behavior on their previous encounter, irrespective of their interaction partner. The requirements are basically the same as before minus the memorizing of who did what; yet, generalized reciprocity, as well as other (more complex) conditional strategies (Szolnoki and Perc, 2012), seem out of reach of the simplest organisms.

An other critical shortcoming of reciprocation mechanisms to explain the advent of grouping features is their dyadic aspect by definition.

1.3.2 Policing (reward / punishment)

Cooperation may be enforced by individuals able to punish free-riders (resp. reward cooperators) (Clutton-Brock and Parker, 1995). The ability to punish (resp. reward) is itself costly. Once again, policing requires the ability for individuals to monitor others’ behaviors and to direct the punishment/reward toward them. Moreover, even though punishment may in principle deter defection, the survival of the cooperative-punisher type is complicated by “second-order free-riders”, i.e. cooperators that do not punish (Sigmund, 2007).

While both theoretical (Boyd et al., 2003) and experimental or observational (Fehr and Gächter, 2002; Flack et al., 2006) studies suggest that policing mechanisms might have an important role in sustaining collective cooperation in humans and other primates, the evidence of punishing/rewarding behaviors in microbes remains at best elusive.

1.3.3 Interactions directed toward genealogical kin

The rough idea behind interactions directed toward kins is encapsulated in this maxim by J.B.S. Haldane: “Would I lay down my life to save my brother? No, but I would to save two brothers or eight cousins”. If for some reason individuals tend to interact mostly with partners that share genes that are identical by descent to their own (i.e. if the actor and recipient are genealogically related), then cooperative behaviors may be promoted if the benefit conferred to kins weighted by the relatedness coefficient between interactants exceeds the cost. This idea is enclosed in the famous rule of Hamilton: $rb > c$, which has remained, since Hamilton’s pioneering work half a century ago, the formulaic rule of thumb to assess the sustainability of helping behaviors in biological settings (Hamilton, 1964). Yet, its generality is recurrently questioned (Nowak et al., 2010a) and its application by mis-informed experimenters and theoreticians often inaccurate. Indeed, the rigorous evaluation of each parameter (r, b and c) is nowhere near as straightforward as posited by some and rely on complex regression coefficient calculations. For instance, population genetics calculations show that the “right” r coefficient does not solely includes genealogical relations, but also the way population is structured and individuals interact. Even though general (as derived from another totem of population genetics, the Price’s equation (Gardner et al., 2011)), Hamilton’s rule might be of little use to describe the conditions for the evolution of cooperation in experiments and analytical models, some claim (Nowak et al., 2010a). Nonetheless, Hamilton’s main point remains a milestone in alleviating the challenge of cooperation for species, as diverse as social insects and many microbial species, characterized by a high level of inbreeding (e.g. generated from a single lineage).

In any case, what Hamilton’s rule does not say is how individuals are led to interact preferentially with their kins. The two main mechanisms invoked in the literature are kin discrimination (crudely: individuals are able to recognize their brothers and sisters and interact predominantly within the family) or spatial structure (when limited dispersal or environment viscosity imply that lineages remain clustered).

1.3.4 Assortment between cooperators

When cooperators tend, for some reason, to interact more with other cooperators than defectors do, they get a higher average benefit from their interactions that may ultimately offset their cost (Wilson and Dugatkin, 1997; Fletcher and Doebeli, 2009). Assortment has some overlap with the previous family of mechanisms (insofar as if cooperating individuals tend to interact with their kins, *de facto* they interact with partners likely to share the cooperative gene), but is more general, the mechanisms liable to make cooperators interact together and not based on shared ancestry being numerous. The tricky part is to find those mechanisms. A key lies in the way populations are structured, in terms of spatial structure and interaction structure, motivating researchers to explore how networks, group shapes etc. influence this degree of assortment (see sections 1.5 and 1.6). A particular case is when cooperators interact together because they can identify each other. We refer to the Box 1.2. for a discussion about this issue.

Box 1.2. Green beards

A “green beard” refers to any gene, or set of linked genes, that encodes at the same time for 1) a given behavior; 2) the ability to recognize other carriers of the green beard; 3) the propensity to direct the behavior preferentially towards these carriers. The term was first used by Dawkins to make a hypothetical claim (Dawkins, 1976), and examples of green beards proved difficult to find until recently. For most of them, the “green beard” label remains controversial and one can argue that the three above requirements are not always fulfilled. Green beards can be either cooperative toward carriers, or spiteful against non-carriers. Examples of proclaimed green beards include (this list is widely inspired by Brown and Buckling (2008)):

- the *csA* gene in Dicty (Ponte et al., 1998; Queller et al., 2003) that encodes a cell adhesion protein that binds to homologous adhesion proteins (cooperative);
- the recognition of kins in *Proteus mirabilis* (Gibbs et al., 2008) (cooperative);
- the FLO1 gene in *S. cerevisiae* (Smukalla et al., 2008) between sticky cells, though cooperating sticky cells can also connect to nonsticky cells, although less probably (cooperative);
- the "queen-killer" allele in red fire ants (Keller and Ross, 1998) (spiteful);
- genes encoding bacteriocins (kind of chemical weapons) that at the same time make their carriers immune to their effect (Riley and Wertz, 2002) (spiteful);

Green beards may be subject to cheating as, very often, a set of linked genes rather than a single gene encodes the "beard": there is thus a risk of invasion by mutants that display the tag without the costly behavior. A retort to this can be found in the possibility of multiple beard colors (Jansen and van Baalen, 2006). For instance, the FLO1 gene is known to be highly variable among species (more or less adhesive). In many cases, it is actually difficult to contend with certainty that a given behavior relates to a green beard. Indeed, the "preferentially directed" condition is not necessarily needed to get behaviors that are differentially directed toward carriers or non-carriers. This subtle difference will be more thoroughly developed later on in chapter 2.

1.3.5 Direct benefits

Although situations in which the evolution of a costly cooperative trait is paradoxical are emphasized in the literature, the evolution of cooperation needs not necessarily be a social dilemma. In some cases, the cost incurred by cooperators is immediately offset by the marginal benefit they get from their own contribution to the group. In the standard Public Goods Games (section 1.4.2), such case would translate as $b > Nc$. In invertase-secreting yeast, a small proportion of the hydrolized glucose is retained by the producer, advantaging cooperator cells at low frequencies (Gore et al., 2009). Similarly, the bacterium *Lactococcus lactis* expresses an extracellular protease that helps transform milk proteins into digestible peptides. Bachmann et al. (2011) showed that such cooperative behavior can persist owing to a small fraction of the peptides being immediately captured by the proteolytic cells.

1.3.6 Game definition

While the Prisoner's Dilemma and variations account for a large portion of the archetypal games used in evolutionary game theory, every social dilemma is actually not as hostile to cooperation. There are other possible game structures allowing to escape from the paradox of the tragedy of commons. Sometimes the hypotheses formulated by evolutionary game theory to untangle the enigma of cooperation make it artificially too challenging compared to real biological situations. For instance, nonlinear payoff profiles that are more consistent with biological settings than the (most often used) linear payoffs can alleviate the paradox and account for the sustainability of cooperative traits very easily, even in the absence of kinship, assortment or external mechanisms.

In the next sections, I review some important findings about the influence of the structure of interactions (i.e., the "game" that is played), the structure of population and the way group are defined on the emergence and maintenance of cooperation.

1.4 Game structure

Evolutionary game theory relies on archetypal (some may say artificial) games to capture the main features of dilemmas encountered in biological populations. Depending on the nature of interactions, these are played between two or an arbitrary number N of players.

1.4.1 Dyadic games

These games relate to pairwise interactions. Individuals can be either cooperators (C) or defectors (D). The interaction results in the allocation of a payoff for each player. Such games can be summarized with this general payoff matrix:

	C	D
C	(R, R)	(S, T)
D	(T, S)	(P, P)

R stands for "reward" (when both individuals cooperate), S for "sucker" (when a cooperator is exploited by a defector), T is the "temptation" to cheat and P the "penalty" for no one cooperating. Depending on the values of R, S, T, P, the expected evolutionary dynamics and equilibria of populations playing the game in couples change drastically. Readers familiar with the archetypal dyadic games (Prisoner's Dilemma, Snowdrift Game, etc.) shall skip the next paragraphs.

The Prisoner's Dilemma Two members of a gang A and B are questioned separately by the police. Cooperating means staying silent; defecting means denouncing the other one to the police. If both cooperate, each serves a 1-year prison sentence; if each one betrays the other, they both serve 2 years. If A betrays B and B stays silent, A is set free and B serves 3 years in prison (and conversely). Therefore, whatever the other guy does, there is a temptation to defect as it warrants the lighter sentence in any case. However, the best result is obtained when both cooperate. This game can be summarized as $T > R > P > S$ (plus $2R > T + S$ in the iterated form). In the previous example, $T = 0$, $R = -1$, $P = -2$, $S = -3$. Collective defection (D, D) is the unique Nash equilibrium (and evolutionay stable strategy) of the game. This game models situations when a cooperator provides a benefits $b > 0$ to its interaction partner but pays a cost $c > 0$; the payoff matrix can then be re-written as:

	C	D
C	$b-c$	$-c$
D	b	0

This game is widely used as a metaphor for any "free-rider" dilemma where cooperation might be exploited by non-contributing individuals. As cooperation is doomed were no other assumption made, it is the most challenging, hence the most investigated of all 2-player games.

The Snowdrift Game (a.k.a. Chicken or Hawk-Dove Game) Two drivers are trapped behind a pile of snow. Someone must shovel off the snow or nobody will come back home; but each driver is better off if the other one does the job. In this game, $T > R > S > P$: the only difference with the Prisoner's Dilemma is that it is still better to do the work by yourself than waiting the other guy to do it in vain. It is thus best to do the opposite of the other player. (C, D) and (D, C) are pure (unstable) Nash equilibria, and there exists a mixed equilibrium that is stable: this means that in populations where the two types compete, the expected evolutionary equilibrium is polymorphic, with one fraction of the population (that depends on the game parameters) cooperating and the rest defecting. In the context when achieving the common goal provides a benefit b and doing the whole work costs c, the payoff matrix can be re-written as, for instance:

	C	D
C	$b-c/2$	$b-c$
D	b	0

The Stag Hunt (a.k.a. Coodination Game:) In this game (less popular in the literature than the two former), individuals must coordinate to achieve a common goal. Therefore, it is best to do as the other player does. The payoffs are ranked as followed: $R > T > P > S$. (C, C) and (D, D) are both (stable) Nash equilibria, and there exists a mixed equilibrium that is unstable. In population settings, the outcome is thus dependent on the initial condition: if the proportion

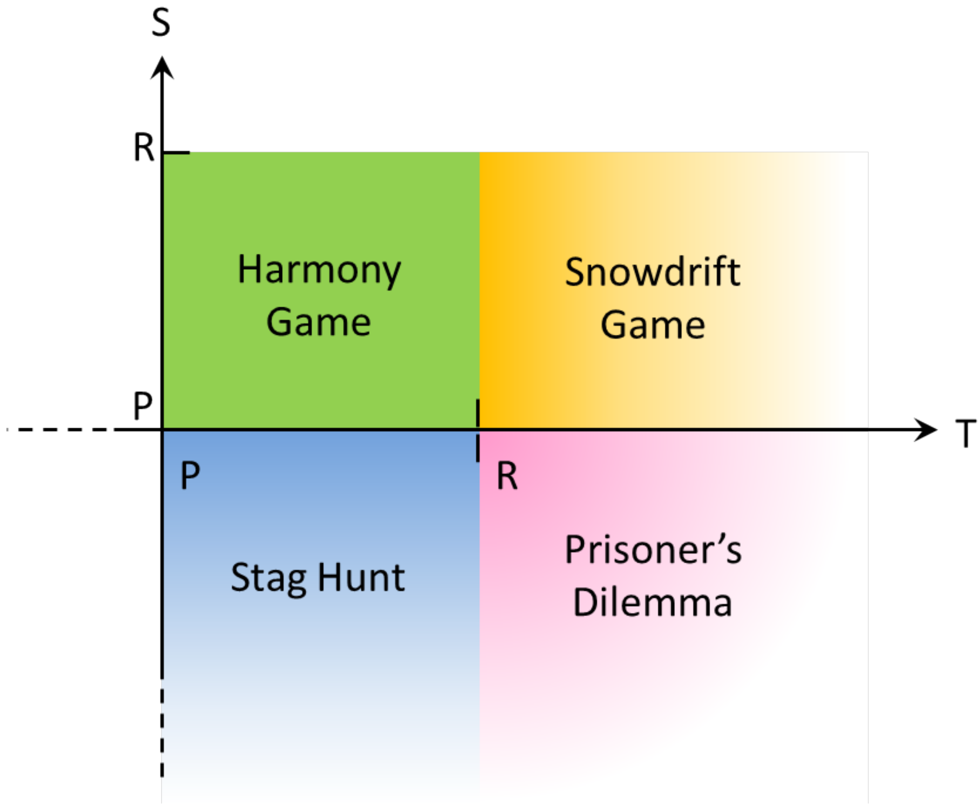

Figure 1.2: Representation of the Prisoner's Dilemma, the Snowdrift Game, the Stag Hunt and the Harmony Game in the (T, S) plane.

of cooperators at beginning exceeds the mixed equilibrium, then the population evolves to full cooperation; otherwise, it evolves to full defection.

The Harmony Game: This game (characterized by either $R > S > T > P$ or $R > T > S > P$) is never (to my knowledge) studied in the literature as it is trivial: (C, C) (collective cooperation) is the unique Nash equilibrium, and there is thus no social dilemma to speak of.

The four games are represented in the (T, S) plane in Figure 1.2.

1.4.2 N-player games

N-player games refer to situations when a group of N players may or may not accomplish a collective outcome that benefits every member depending on the number (or the fraction) of cooperators in the group. N-player games are inherently irreductible to the corresponding sum of dyadic interactions, and are as such different social dilemmas (Perc et al., 2013). In the most basic case, the population is well-mixed and players meet at random.

The Public Goods Game: The Public Goods Game (PGG) can be seen as a logical extension of the Prisoner's Dilemma to interactions between N players. The principle is the following: each cooperator contributes b to a common goods at a cost c to their fitness; defectors contribute nothing, and do not undergo any cost. The sum of all contributions in the group is then shared equally among all members, irrespective of their strategy. The respective payoffs of a cooperator and a defector, provided m of its $N-1$ co-members cooperate and $N-m-1$ free-ride, are thus

$$P_C(m+1, N) = b\,\frac{m+1}{N} - c \tag{1.1}$$

and

$$P_D(m, N) = b\,\frac{m}{N} \tag{1.2}$$

Let us now suppose that individuals in the population are randomly distributed into groups of size N, and let us call x the frequency of cooperators in the population (then, $1-x$ is the frequency of defectors). The expected payoffs $P_C(N)$ and $P_D(N)$ of each strategy are calculated summing the payoffs obtained in the situation when there are m cooperators among the $N-1$ co-players weighted by the probability $\binom{N-1}{m}\,x^m\,(1-x)^{N-1-m}$ of it happening with random sampling. The average payoff difference between cooperators and defectors is thus

$$\begin{aligned}
\Delta P &= P_C(N) - P_D(N) \\
&= \sum_{m=0}^{N-1} \binom{N-1}{m} P_C(m+1, N)\, x^m (1-x)^{N-1-m} \\
&\qquad - \sum_{m=0}^{N-1} \binom{N-1}{m} P_D(m, N)\, x^m (1-x)^{N-1-m} \\
&= \sum_{m=0}^{N-1} \binom{N-1}{m} \left[b\frac{m+1}{N} - c - b\frac{m}{N} \right] \\
\Delta P &= \frac{b}{N} - c \qquad (1.3)
\end{aligned}$$

Therefore, under random allocation of players within groups, ΔP does not depend on x. Generally, $b < Nc$ is assumed, so that the evolution of cooperation is challenging. Otherwise, cooperation evolves simply by direct benefits. A way to represent PGGs in cases other than random allocation uses the concept of *average interaction environments* (Box 1.3.)

Box 1.3. Average interaction environments

I here present the formalism of Fletcher and Doebeli (2009), which will be useful in chapter 2. An individual's payoff can be split between a payoff due to self ($b/N - c$ for cooperators, as they get a share b/N of their own contribution and pay a cost $-c$, and 0 for defectors) and a payoff due to the group co-members ($b/N \times$ the number of cooperative co-players).

Let us denote e_C and e_D the average number of cooperative co-players in a cooperator's (resp. defector's) group, then the average payoffs of a cooperator and a defector are:

$$\begin{aligned}
P_C &= b\,\frac{e_C}{N} + \frac{b}{N} - c \\
P_D &= b\,\frac{e_D}{N}
\end{aligned}$$

Therefore, if the cooperative trait has no effect on the groups an individual encounters, there is no assortment between cooperators and defectors and $e_C = e_D$: cooperation outcompetes sociality only when $b/N > c$, i.e. if cooperation provides a direct benefit to the actor. This case is usually discarded as trivial in models addressing the evolution of cooperation. When $b/N < c$, cooperation vanishes at the evolutionary equilibrium. Hence, for cooperation to be maintained, thus must be a way to obtain $e_C > e_D$ (positive assortment).

Non-linear games (e.g. the "Volunteer's Dilemma") In the standard PGG, the benefit derived from the group varies linearly with the fraction of cooperating members, which can seem arbitrary and dissimilar to actual biological situations (Cornforth et al., 2012). Archetti and Scheuring (2012) point out that, in microbes that cooperate secreting a diffusible enzyme outside their membrane, individual benefits are most often a saturating or sigmoid function of the enzyme concentration. Non-linear payoffs rather than linear functions can thus be used, the extreme case of which are step functions of the number (or fraction) of cooperators in the group. The core idea of the Volunteer's Dilemma (Archetti and Scheuring, 2010) – to be distinguished from "voluntary participation" (Hauert et al., 2002a,b) – can be sketched as follows: group members get a payoff b as soon as at least N^* cooperators are present in the group. Otherwise, everyone gets a null payoff from the group. As before, cooperators pay a cost c for their contribution. Provided m of their $N-1$ co-members cooperate, a cooperator and a defector will get respectively

$$P_C(m+1, N) = b\,\delta_{m+1 \geq N^*} - c \tag{1.4}$$

and

$$P_D(m, N) = b\,\delta_{m \geq N^*} \tag{1.5}$$

where

$$\delta_{condition} = \begin{cases} 1 & \text{if } condition \text{ is met} \\ 0 & \text{otherwise} \end{cases} \tag{1.6}$$

In the case of random allocation of individuals into groups of size N, the expected payoff difference is then

$$\begin{aligned}
\Delta P &= P_C(N) - P_D(N) \\
&= \sum_{m=0}^{N-1} \binom{N-1}{m} \left[P_C(m+1,N) - P_D(m,N)\right] \, x^m (1-x)^{N-1-m} \\
&= b \sum_{m=N^*-1}^{N-1} \binom{N-1}{m} x^m (1-x)^{N-1-m} - c \\
&\qquad - b \sum_{m=N^*}^{N-1} \binom{N-1}{m} x^m (1-x)^{N-1-m} \\
\Delta P &= b \binom{N-1}{N^*-1} x^{N^*-1} (1-x)^{N-N^*} - c
\end{aligned} \tag{1.7}$$

Figure 1.3 displays the payoff difference ΔP as a function of the cooperator frequency x. When x is too low, the amount of cooperators N^* required to trigger the common goods b is unlikely to be reached, so that being a cooperator is unprofitable on average. Conversely, when x is high, it will most likely be reached anyway so that it is no use to contribute from the point of view of a focal player. As a consequence, ΔP is positive in a range $[x_{thres}, x_{poly}]$, where the incentive is strong enough to justify cooperation. In addition to stable equilibria $x = 0$ and $x = 1$, the replicator equation has thus one unstable equilibrium x_{thres} and one stable polymorphic equilibrium x_{poly}. This means that as soon as a frequency x_{thres} is reached in the population, cooperators rise in frequency until $x = x_{poly}$ and the stable population is a mixture of cooperators and defectors.

The lesson to be learned from this simple game is that even in the absence of kinship and assortative mechanisms, a certain level of cooperation may be stable provided benefits retrieved

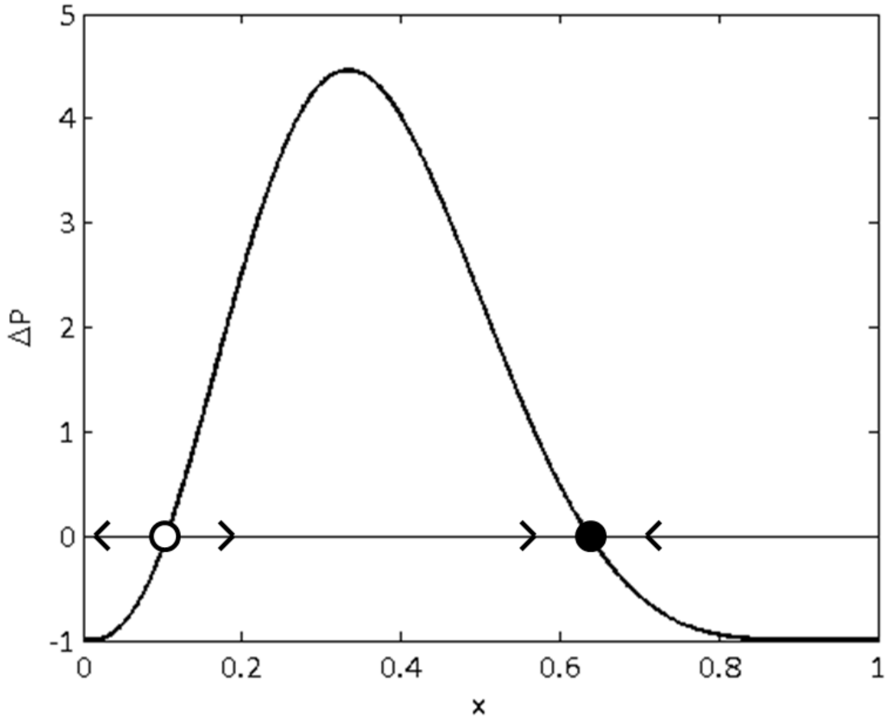

Figure 1.3: Payoff difference between cooperators and defectors in a threshold game.

Apart from the absorbing states $x = 0$ and $x = 1$, the game has two interior equilibria, one unstable and one stable. Thus, cooperation rises in frequency from a threshold value x_{thres} until it reaches a value x_{poly}. Parameters values: $b = 20$, $c = 1$, $N = 10$, $N^* = 4$

from groups do not increase linearly (Archetti and Scheuring, 2012). While a plausible explanation for the persisting presence of helping behaviors in biological populations, this way out of the puzzle of cooperation might be nuanced in the case of large groups, as the range where cooperation is promoted shrinks when group size increases given a fixed benefit-to-cost ratio b/c (Fig. 1.4).

1.4.3 The difficulty finding the right game

How biological dilemmas relate to such abstract games is often unclear. In an interesting experiment on yeast, Gore et al. (2009) claim to have found a microbiological instance of a Snowdrift Game (SD). Wild-type yeast breaks the sucrose in their medium into fructose and glucose they

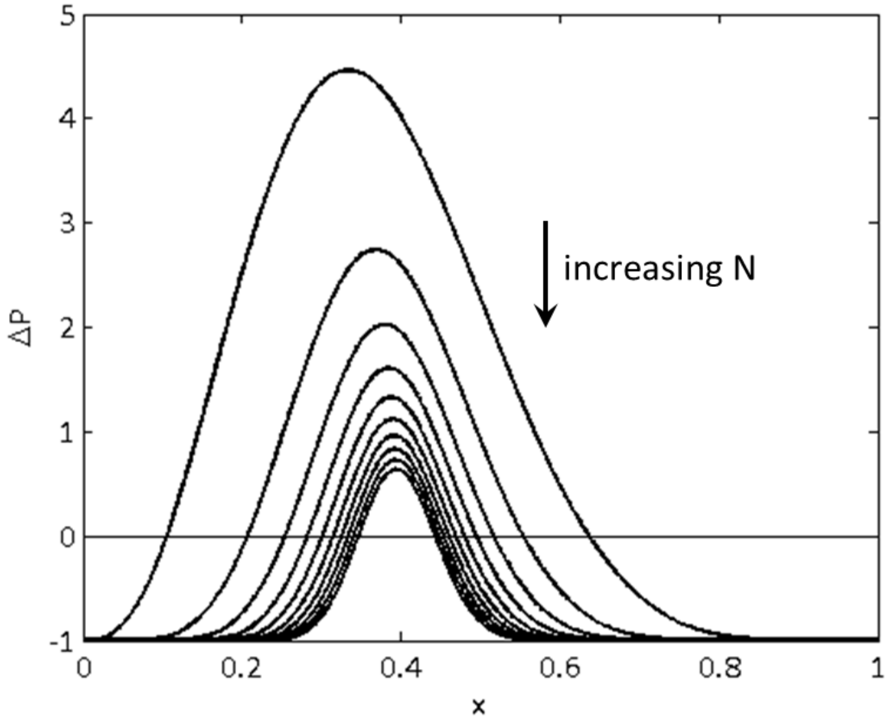

Figure 1.4: Payoff difference between cooperators and defectors in a threshold game when N varies.

Cooperation has to reach an increasingly higher threshold frequency as the group size increases, and when it does it stabilizes to smaller frequency equilibrium levels. Parameters values: $b = 20$, $c = 1$. N ranges from 10 to 100, and the threshold N^* is kept proportional to N (thus ranging from 4 to 40).

can more easily feed on. However, while doing so, 99% of the glucose and fructose escape diffusing in the medium when only 1% is imported in the cytoplasm of the invertase-producing cell, therefore exposing the producing type to exploitation by nonproducers. Gore et al. (2009) mixed one WT cooperative strain of yeast and one mutant defective type lacking the invertase gene, with various starting frequencies of each. They found out that each type tends to rise in frequency when initially rare, reaching an equilibrium level that depends only on the cost of cooperation, and not on the initial frequencies. They explain that the growth rate is a concave function of glucose, that is, marginal growth gains for getting more glucose tend to decrease as its concentration increases. Therefore, defectors, that have a hard time to thrive when cooperation is rare, can persist when it reaches a threshold level in the population and outcompete them for high levels. The authors interpreted such striking example of coexistence between cooperators and defectors as the effect of a SD played between yeast cells. However, this conclusion is debated. Archetti and Scheuring (2012) assert that the SD is inappropriate to account for such instance of frequency-dependent selection as it is primarily a 2-player game, unlike interactions in yeast. They also point out that in the SD, the maximal cumulated payoff for all players is obtained in the case of total cooperation (citing MacLean et al. (2010)), while the experiments found that the maximal value for the total population growth was obtained for an intermediate frequency of producers. Their two points are however questionable:

1) The SD can be easily extended to N-player interactions. Coming back to the metaphor that gives its name to the game, if N^* cooperators are required to shovel off the snow, the payoff assigned to a cooperator (resp. defector) in the N-player SD game could be, if there are m cooperators within the $N-1$ focal player's co-members:

$$P_C(m+1, N) = b\,\delta_{m+1 \geq N^*} - \frac{c}{m+1} \tag{1.8}$$

and

$$P_D(m, N) = b\,\delta_{m \geq N^*} \tag{1.9}$$

However, general formulations of the SD such as the former generally imply that the cost payed by a cooperator decreases with the number of cooperators within the group (here, $c/(m+1)$); it is unsure wether or not such property applies to invertase production in yeast.

2) The maximal cumulated payoff for all players is not necessarily obtained in the case of total cooperation: while it does so for the usual, handbook payoff matrix of 2-player SD (in which the cost payed by each of two interacting cooperators is half that of the cost payed by a cooperator alone), such assertion does not hold anymore – as MacLean et al. (2010) themselves observe – for variants that are still SDs, e.g. games represented by the payoff matrix

	C	D
C	$b - 2c/3$	$b - c$
D	b	0

Here, taking the standard algebraic formulation of a game too literally might lead to discard a hypothesis on erroneous grounds.

Even before, the yeast dilemma was identified as a Prisoner's Dilemma (Greig and Travisano, 2004), but the experiments described above somewhat debunk this claim. If anything, this example illustrates that the mapping of evolutionary game theory with experiments on real biological organisms is nowhere near straightforward.

1.5 Population structure

Since the seminal work of Nowak and May (1992), it has been clear that the way population is structured is crucial to the evolutionary fate of a cooperative trait (Sumpter, 2010), compared to a well-mixed situation where each player interacts with any other player with equal probability. By "population structure", we mean the network (in the broad sense) of interactions occurring between individuals, be they pairwise when dyadic games are played, or within a group or a set for N-player games (Nowak et al., 2010b). Most often, this interaction network will stem from spatial structure: individuals who are close tend to interact together more. Sometimes (in models with synthetic graphs), the focus is not on spatiality but on the way links between individuals are globally distributed (e.g. is the network regular, random, small-world, scale-free, etc; see Watts and Strogatz (1998); Barabási and Albert (1999)).

1.5.1 Lattices

Regular lattices have been the first tool used for the systematic study of population structure's influence on the evolution of cooperation, first and foremost regarding 2-player games. In (Nowak and May, 1992), each site is occupied by one player, either a cooperator or a defector. Every generation, each individual plays a Prisoner's Dilemma with its immediate neighbors, and its total payoff is the sum of payoffs in each game. Population is updated changing the strategy in each site to that of the most successful player in the neighborhood. Nowak and May (1992) showed that such simple rules suffice to obtain coexistence between cooperators and defectors in a large range of parameters, as well as a wide variety of spatial patterns, from stable cooperating clusters in a sea of defectors to chaotic "Turkish carpet"-looking repartition of each type on the lattice. Possibly owing as much to the beauty of the figures as the main message (spatial structure is key to facilitate the stability of cooperation), this work has stimulated an important amount of work to explore the dynamics made possible by more convoluted strategies, lattice structures, or update rules, to such an extent that the field of the evolution of cooperation in spatially-structured populations has taken a life on its own (some would lament, faraway from realistic biological settings, e.g. Leimar and Hammerstein (2006)). Since then, the main properties of the PD on lattices have been thoroughly explored, and the ability for players to be mobile, tested (e.g. by Vainstein et al. (2007); Roca and Helbing (2011)). The main idea to retain from this subset of the literature on social evolution is that spatial structure may generate self-organized clusters of cooperators that are robust to exploitation at their border. Or, more crudely: spatiality may generate assortment between cooperators (or relatedness – in the broad sense of the word –, depending on who is talking). The range of parameters in which cooperation survives is itself dependent both on the update rule (deterministic or stochastic) and the lattice clustering coefficient. When N-player, rather than dyadic games, are played however (e.g., when each player takes part in k Public Goods Games, k being the degree of the lattice), the topological properties of the lattice become irrelevant because group interactions effectively link non-directed connected players together. I refer to Doebeli and Hauert (2005) and Perc et al. (2013) for reviews on social evolution on lattices.

1.5.2 Graphs

Lattices define very constrained interaction structures. To disentangle the effects of spatial structure implied by lattices from that of the number of neighbors of each individual, researchers have implemented evolutionary games on random homogeneous graphs (i.e. where each node has the same number k of links). They evidenced that it makes little difference with lattices on the equilibria obtained when the game is a Prisoner's Dilemma, though it favors cooperation in the Stag Hunt and inhibits it in the Snowdrift Game (Roca et al., 2009). More dramatic is the effect of degree heterogeneity ("heterogeneous graphs"). Santos et al. (2006) showed that the more heterogeneous is the pattern of connectivity, the more cooperation is likely to take over. Pinheiro et al. (2012) indeed showed that individuals playing the Prisoner's Dilemma at the microscopic level in a structured population was somewhat equivalent to them playing a Snowdrift Game (in homogeneous networks) or a coordination game (in heterogeneous networks) at the macroscopic (population-wide) level. The same team then pushed the analysis to N-player games (Santos et al., 2008). In their model, each node i plays k_i Public Goods Games, where k_i is its degree. They tested two different cases: (1) the cost applies to each case (i.e., the more links a cooperator has, the higher the cost); (2) the cost is fixed for one player (i.e., a cooperator divides a fixed cost c between all its links). Their work shows that cooperation is enhanced for heterogenous networks (compared to regular graphs) because of the major influence of cooperative hubs, and that it does so in a larger parameter range in case (2) than in case (1). As for lattices, the science of network cooperation has bloomed since then; notably, many studies have implemented complex degree-based policies for cooperation, as well as the possible coevolution of cooperation and link formation (see the reviews by Perc et al. (2013) and Perc and Szolnoki (2010), respectively).

1.5.3 Continuous space

More recently, models have started to consider pairwise or group interactions as emerging from the spatial reallocation of mobile individuals in a continuous 2D space. The purpose of these models is twofold: 1) they allow to specify the origin of interactions in a more realistic way. Indeed, most social organisms are mobile (from microbes such as Myxobacteria to humans) and by moving they find new interactions; models in continuous space can thus in principle draw inspiration from real life data on motion and be implemented within an evolutionary framework. Theoretical descriptions of animal aggregation are commonplace in fields such as ecology or statistical physics, but are only beginning to permeate social evolution theory. 2) They are instrinsically dynamic, unlike lattices models in which groups are fixed and most models on graphs (except coevolutionary models or cases when a specific grouping behavior is associated to cooperation, e.g. in Pacheco et al. (2006)): the emphasis made on movement implies that an individual's interaction network may change at each time step. Meloni et al. (2009) designed a model where individuals, either cooperators or defectors, are mere random walkers that play a Prisoner's Dilemma with their neighbors within some radius at each timestep. Individuals update their strategies imitating one of their neighbors with a probability that depends on the difference of their payoffs. In this simple setting, cooperation is able to arise thanks to cooperative clusters forming by chance and slowly expanding by successive victories against defective individuals in their immediate surroundings. Later, Cardillo et al. (2012) expanded this framework to Public Goods Games. Another set of rules for movement based on flocking in birds has been used by Chen et al. (2011a,b). Note that in all these models, the groups in which the games are played overlap (cf. section 1.6.2), and movement is uncorrelated from the evolutionary dynamics, unlike some models on lattices. A model of aggregation where these two assumptions are relaxed will be described in chapter 3 of this manuscript to study the evolution of social adhesion traits.

1.6 Group structure

1.6.1 Groups as equivalence classes

Possibly inspired by the ecological literature, many models for the evolution of cooperation consider groups as separate entities, with, possibly, occasional migration between them. This assumption is in accordance with many biological systems, such as animals foraging in distinct herds, or slime moulds, to name but a few examples. Actually, an important part of the theoretical literature in the field deals with competing individuals within competing groups, raising the issue of potential conflicts between levels of biological organization (Wilson, 1975; Chuang et al., 2009). The range of models that explicitely assume groups as a partition (in the mathematical sense) of the population is too large to review it properly in a few lines; among these works, let us cite arbitrarily the papers by Wilson and Dugatkin (1997); Avilés (2002); Hauert et al. (2002a); Fletcher and Zwick (2004); Killingback et al. (2006); Traulsen and Nowak (2006); van Veelen et al. (2010); Powers et al. (2011); Cremer et al. (2012). A notable feature of most models with separate groups (though exceptions can be found in those just mentioned) is that they assume group size is fixed. What is a convenient hypothesis for analytical calculations may however obfuscate the role of distributed group sizes on the onset and maintenance of cooperative traits, as pointed out by Peña (2012), who studied games in groups of cooperators and defectors obeying an externally imposed size distribution. I refer to the small opening review of chapter 2 for a discussion of works displaying varying group sizes.

1.6.2 Groups as sets

Rather than considering groups that are separate, non-overlapping entities, recent work suggested that allowing individuals to belong to several groups at a time may be more relevant to address social dilemmas. This observation is particularly appropriate for us humans, as we tend to take part in numerous collective activities, be they within the family, at work, or in our leisure time. Under this hypothesis, groups are called "sets" and the encompassing framework "evolutionary set theory" (Tarnita et al., 2009). Sets can in principle be of any size and one set can be a subset of an other set. Tarnita et al. (2009) designed a model in which individuals play the Prisoner's Dilemma in a set structure and where both their strategy (cooperator or defector) and their set membership are subject to updating through imitation. They calculated the critical benefit-to-cost ratio from which cooperation outcompetes defection in the particular case when individuals all belong to the same number of sets K. They showed that, given a number of sets M in the population, cooperation evolves more easily the smaller K is. This result is relaxed when cooperators only cooperate provided they share a minimum number L of sets with their partners: in this case, belonging to more sets proves advantageous to evolve cooperation. It is difficult, though, to assess the scope of such theoretical in non-human animals and, *a fortiori*, microbial communities, as the initial assumptions of individuals belonging to several distinct collective endeavors is not much discussed empirically. Indeed, even though microbes do participate in several social dilemmas at once (e.g. Myxobacteria or *Pseudomonas* mentioned above), the model of Tarnita et al. only makes predictions in the case when cooperation applies the same way to each of them (i.e., an individual is either cooperative in all sets or defective in all sets). Cooperative behaviors in microorganic populations rather relate to different mechanisms at the molecular level: a cell is not cooperative or defective *per se*, but relative to one specific social need (and, arguably, to a specific ecological context, but this is out of the scope of my discussion).

1.6.3 Non-delimited groups

In some theoretical works on social evolution, there is no defined group, although the interactions are not dyadic either: instances of these are models of individuals producing a public goods substance in their medium that is available to all individuals in the vicinity. Such models are more readily comparable to biological situations such as *Pseudomonas* competing for the access to siderophores. Driscoll and Pepper (2010) have developed a general framework that combines the physics of diffusion with a game-theoretical model. They show that the success of the “producer” type depends on the diffusion coefficient of the secreted compound and its uptake rate. Low diffusions favor producers as they prevent the substance to be shared too much with defectors, enabling production to evolve by direct benefits; similarly, high uptake rates ensure that producers deplete the substance sufficiently for themselves before it reaches the free-riding nonproducers. This work makes an important point stressing the continuum between private and public goods, and that public goods, non-excludable as they are, may in some conditions provide enough direct benefits to offset production costs. Here, spatial structure and environment viscosity entail that the goods is differentially shared with others according to their distance. In an other instance of model for the diffusion of a resource in space, Borenstein et al. (2013) challenge the conclusions of classic spatial models displaying frequent coexistence of cooperators and defectors by spatial clustering of uninvadable clusters of cooperators. They claim that the main assumption of such works, namely the nearest-neighbors interaction rule, artificially generates coexistence while more realistic hypotheses generate longe-range interaction that disrupt it.

1.7 Outline

In this work, I will try to assess the conditions for the emergence and persistence of an individually costly trait that enhances grouping tendency and supports group cohesion. This will lead me to emphasize the mechanics of aggregation as a decisive feature – yet generally overlooked in the literature – for the sustainability of social traits. More specifically, the following questions will be addressed:

- how does selection act on population structure through the traits underpinning group formation?

- how do the structure of the population and its social composition feed back onto each other?
- is the existence of a biologically trait that at the same time enhances individual attachment and benefits groups plausible?
- what if sociality is a continuously regulated feature, rather than an on/off individual characteristic?
- is the "social dilemma" necessarily a dilemma? How does it relate to population structure?
- what are the microscopic features that promote, or hinder sociality?
- is preferentially directed attachment to carriers of the social trait necessary for social individuals to persist?
- to what extent are the modeling results consistent with observations on actual microbial population structures?

In chapter 2, I describe a general framework to assess the evolution of a social trait in an arbitrary group formation configuration, using group size distributions experienced by distinct social types as a proxy to infer their evolutionary fates. I introduce a toy model for aggregation to pinpoint how costly sociality can evolve with minimal hypotheses for individual interactions, suggesting a mechanistic scenario for its emergence ahead of more sophisticated collective behavior. I then explore the evolutionary dynamics under weaker hypotheses, namely by relaxing the coupling between aggregation and in-group behavior and the characterization of sociality by a discrete trait.

In chapter 3, I embed the former framework in a generic class of group formation processes intended to capture the main features of microbial aggregation. I decipher the evolutionary outcome of a social mutation by means of appropriately defined macroscopic observables reflecting the social composition of the population. I precise the ecological and microscopic conditions on individual motion and interaction necessary to support sociality. Finally, I relax the hypothesis of the existence of a pre-defined life cycle assumed until then.

In chapter 4, I discuss the main results of chapters 2 and 3 in the light of the aforementioned questions, and sketch possible extensions of the work and open questions.

Chapter 2

Group formation and the evolution of sociality

Sections 2.1, 2.2, 2.3 and parts of the discussion are adapted from “Garcia, T., and De Monte, S. 2013. Group formation and the evolution of sociality. Evolution, 67, 131-141.” The analysis of section 2.5.4 was performed in collaboration with Guilhem Doulcier during his internship in the lab. He also made Figures 2.10 and 2.11 and the computer code to generate them.

2.1 Introduction

The emergence and persistence of social ventures, where individuals concur to the sustainment of a community at a personal cost, has been classically addressed in a game-theoretical framework. The evolution of cooperation was first formalized in the context of dyadic interactions, where the formation of pairs and the accomplishment of the game are concomitant. When individuals play in couple, several mechanisms effectively promote cooperation even for a Prisoner’s Dilemma type of interactions, where it is always in one own’s interest to defect in a single round of the game (cf. section 1.4.1). Cooperators can thrive provided they interact preferentially with other cooperators, e.g. via the knowledge of the co-player's past behavior (Trivers, 1971; Axelrod and Hamilton, 1981), reputation (Nowak and Sigmund, 1998), spatial structure (Nowak and May, 1992), or mechanisms enhancing individuals' interactions with kins (Hamilton, 1964).

Those results have then been extended to games involving $N > 2$ players, where the Public Goods Game (PGG) plays the same prototypic role as the Prisoner's Dilemma (Kollock, 1998; Doebeli and Hauert, 2005). The PGG formalizes the so-called tragedy of the commons (Hardin, 1968; Rankin et al., 2007), whereby cheaters who do not contribute to the public goods are always better off, in a one-shot game, than cooperators who pay a cost to sustain the collective entreprise (cf. section 1.4.2)

Sociality, however, relates not only to the act of helping others, but also affects the context where social games are played, among which the way groups are formed in the first place. In extending the framework from 2-player to N-player games, the processes that lead to group formation have often been overlooked and group size generally held constant.

This assumption has been recently relaxed in different ways. Group size variations can be externally forced by imposing bottlenecks that periodically increase the variance among groups (Chuang et al., 2009), leading to a "Simpson's paradox" in which cooperation is disavantaged locally but a winning strategy on the whole (Wilson, 1975). They can also result from demographic fluctuations (Hauert et al., 2006a) or facultative participation to the game (Hauert et al., 2002a,b). The effect of a fixed group size distribution with binomial allocation of individuals within groups has also been investigated in various types of games and can either promote or hinder cooperation (Peña, 2012).

Group size can be directly affected by traits that co-evolve with cooperation. Pfeiffer and Bonhoeffer (2003) illustrated how group clustering (defined in terms of spatial proximity) is selected together with nonexploiting, cooperative behavior if resources are sufficiently concentrated. Avilés and co-workers (Avilés, 2002; van Veelen et al., 2010) showed that grouping tendency and cooperativeness may be favored jointly, resulting in the emergence of viable cooperative groups. This result relies on two features of the model: on the one hand, while cooperation is costly, the ability to join groups is not ; thus, as soon as some cooperators are present in the population, individuals are better off in a group than alone, making the lonely lifestyle unprofitable and the dispersed population structure unstable. On the other hand, the introduction of a hump-shaped fitness function implies from the start the existence of intermediate optimal group sizes, at fixed average level of cooperation within the group. The cheating load is then twofold: "freeloaders" both hamper the benefits retrieved from the group and crowd them uselessly. Powers et al. (2011) similarly evidenced that inheritable aggregative features may evolve together with cooperation. They let players have a clear-cut group size preference, whereby groups form by gathering individuals that share the same preference. In their model, cooperation ends up being tightly linked with small group sizes that support it more easily, even when direct selection pressures for large groups or weaker selection against cooperation is applied.

In line with these studies, I address here the evolution of aggregative traits in a context that is dynamically shaped by the traits themselves. Such traits require an individual investment and produce collective benefits, and can therefore be regarded as cooperative once individuals have been allocated in groups by the aggregation process. The quest for simple mechanisms that allow grouping tendency to evolve is of particular relevance to understand sociality in microrganisms, where individuals interact in clusters of many individuals, a setting that is recognized as unfavorable to social ventures (Olson, 1971). In this model, individuals have different propensities to form cohesive aggregates, and group cohesion itself is a common good. Individuals are endowed with a unique gene that codes for a costly trait (coined hereafter *sociality*). The social trait promotes aggregative cohesion during both the group formation process and the reproductive stage, where the fitness is the individual payoff in a PGG. The outcome of the social interaction is thus considered to hinge upon the physical properties of the groups: more cohesive groups are fitter than groups weakened by looser attachment of their members.

This setting is relevant at least for several microbial organisms usually taken as examples of primitive social behavior (Crespi, 2001; West et al., 2006; Smukalla et al., 2008; Nanjundiah and Sathe, 2011), where physical stickiness is coupled to cooperative behavior once aggregates are formed. For instance, in *D. discoideum* populations, chimeras composed of aggregative wild type (WT) and non-aggregative mutants produce slugs whose motility increases with the proportion of WT cells (Inouye, personal communication). In *D. discoideum*, slug motility allows more effecient chemo- and phototaxis, benefiting all cells equally. In Myxobacteria as well, WT's social motility multigene system enables cell clumping. The presence of mutants deprived of this social ability impairs swarming and ultimately mar individual fitness in the group.

To evolve, an altruistic trait must ultimately entail some kind of assortment between its bearers (Fletcher and Doebeli, 2009). When the gene giving rise to such assortment also codes for cooperative behavior, it is framed under the term of "green beards" (Dawkins, 1976; Gardner and West, 2010) (see Box 1.2.). This general definition actually brings together very different mechanisms able to generate assortment, based or not on direct recognition of others' traits. Here, no recognition is involved but assortment emerges spontaneously from blind interactions among individual players. The environment is in this case shaped by the group formation process and changes jointly with the frequency of the social strategy. The advent of sociality stems from merely quantitative differences in the probabilities of attachment, so that even mechanisms that do not produce assortment within groups of fixed size can lead to its evolution if group sizes are distributed.

Section 2.2 describes the evolutionary consequences of group formation schemes where social and asocial individuals differ quantitatively in their ability to aggregate. Group formation is considered a "black box" generating the group size distributions experienced by players. The average fitness advantage of sociality depends on the distributions of group sizes experienced by players of each strategy. I derive the condition for sociality to outcompete asociality under the assumption that no nepotistic grouping between social individuals generates assortment *a priori*. Section 2.3 applies the results of section 2.2 to a toy model based on differential attachment and shows that full sociality in a population can be attained, along with sizeable average group sizes, as soon as a threshold frequency of socials is overcome. The role of lonely individuals, usually neglected when fixed group sizes are considered, is also stressed in the balance of benefits and costs of the social game. I eventually point out that the described mechanism for explaining sociality does not condemn large social groups, and may thus be relevant to account for sociality in microorganisms. Different interaction rules leading to nonzero *a priori* assortment are briefly addressed by numerical simulation. In section 2.4, I relax the hypothesis made on the coupling of sociality in the aggregation phase and cooperation in the PGG considering four distinct strategies. In section 2.5, I adapt the model to the case when the social trait can vary continuously and the evolutionary dynamics is computed in an adaptive dynamics framework. In section 2.6, I discuss the implications of these results for biological systems and the perspectives in elucidating the mechanistic basis of group formation processes.

2.2 General formulation

2.2.1 Hypotheses

It is assumed that group formation happens at a much faster time scales than evolutionary changes. Individuals undergo life cycles that consist of 1) a phase of aggregation; 2) a phase of differential reproduction that modifies the frequencies of each type in the following generation; 3) a dispersal phase (see Fig. 2.1). The whole population is re-shuffled at each generation, unlike models involving lasting groups (Fletcher and Zwick, 2004; Killingback et al., 2006; Traulsen and Nowak, 2006). Sociality consists primarily in a quantitative difference in the ability to aggregate, that affects both the group formation phase and the competitive success of aggregates. Once groups are formed, their cohesion constitutes a public good, so that groups composed of a larger fraction of cohesive individuals confer more benefits to their members.

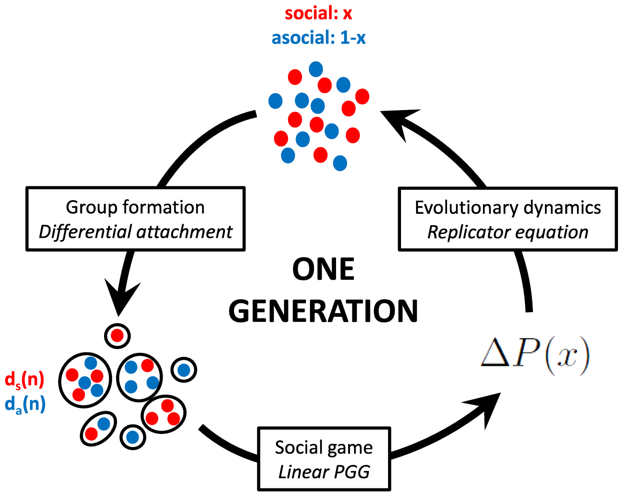

Figure 2.1: Life cycle used in the model

At each generation, we distinguish three processes: aggregation, trait frequency evolution and dispersal (arrows). Initially scattered individuals undergo a group formation process giving rise to groups of different sizes. Differences in attachment ability between the two strategies result in distinct distributions d_s and d_a experienced by players. A social game takes place within each group in the form of a linear Public Goods Game where social individuals contribute to group welfare. The performance of the two strategies is computed in terms of the difference in average payoff. The frequency of the social type x is updated according to this payoff difference and groups are dispersed. If the aggregation phase occurs on a fast timescale with respect to the change in frequency of the two strategies, such evolutionary dynamis can be described by a continuous-time replicator equation.

Individuals are either social (**S**) or asocial (**A**), these two strategies being genetically encoded. **S** individuals pay a cost c for enhanced aggregation. **A** individuals do not pay this cost and have a lower probability to aggregate. After group formation has occurred, both **S**s and **A**s may either belong to a a group or remain alone. For the sake of generality, the grouping process is not specified explicitly but characterized it by its outcome: the distributions $d_s(n)$ and $d_a(n)$ ($n \in \mathbb{N}^*$) of group sizes as experienced by **S**s (resp. **A**s), or “insider’s group size”, or “crowding” (Jarman, 1974; Reiczigel et al., 2008). During group formation, assortment may arise within groups. For instance, processes leading to positive within-group assortment of **S** individuals may rely on preferential interactions (Wilson and Dugatkin, 1997), or on a probability to join a group proportional to the number of **S**s it contains (Avilés, 2002). In this section, I point out that whereas some kind of assortment is necessary for sociality to evolve, no preferentially assortative feature needs to be assumed *a priori* as soon as the group size is not fixed; as such, it is compatible with the scenario where groups form by random and blind interaction processes.

Once groups are assembled, **S** players contribute b to a linear Public Goods Game (PGG), whereas **A** players do not contribute. In a group of size n with m social players, all individuals thus gain $b\,m/n$ irrespective of their strategy. Different choices of the gain function (notably accounting for discount or synergy, as in Hauert et al. (2006b); Archetti and Scheuring (2010); Cornforth et al. (2012)) are possible, but I opt here for the standard linear formulation, so as to focus only on the nonlinearities generated by the aggregation process. Thus, no group size is inherently beneficial to group members, and the payoff only depends on the proportion and not on the absolute number of **S**s in a group. This is a conservative hypothesis since any payoff function increasing with group size would be further favored whenever sociality is associated with larger groups.

2.2.2 Payoff difference for a general aggregation process

Let us compute the average payoff of each strategy in a population where a fraction x of individuals is social and a fraction $(1-x)$ is asocial. After the aggregation process, **S**s and **A**s belong to groups of variable sizes. A PGG is played within each group, and the resulting average payoffs for both types determines the change in their frequencies at the next generation.

Consider first groups of size n $(n \geq 2)$. Following Fletcher and Doebeli (2009), individual payoffs are split in a part due to self and an other due to the interaction environment, that depends only on the composition of the group (Box 1.3.). The payoff due to self is $b/n-c$ for an **S** player, who pays a cost $-c$ for sociality and gets a share b/n of its own contribution to the common goods; for an **A** player, who does not contribute to the PGG, it is 0.

For a linear PGG, the payoff due to the interaction environment is proportional to the average number $e_s(n)$ (resp. $e_a(n)$) of **S**s among the $n-1$ coplayers of an **S** (resp. **A**) player, so that the average payoffs of **S** individuals in a group of size n is:

$$P_s(n) = \frac{b}{n}\, e_s(n) + \frac{b}{n} - c \tag{2.1}$$

and for **A**s:

$$P_a(n) = \frac{b}{n}\, e_a(n) \tag{2.2}$$

The "interaction neighborhoods" $e_s(n)$ and $e_a(n)$ are in general different, e.g. if assortative mechanisms such as peer or group recognition are involved in the process of group formation. In these cases, the local environment of a **S** player is enriched in **S**s compared to that of an **A** player ($e_s(n) > e_a(n)$). For instance, total segregation between **S**s and **A**s would yield $e_s(n) = n - 1$ and $e_a(n) = 0$.

Considering all possible group sizes, the payoff for **S** and **A** individuals is obtained as an averaged sum of these payoffs, weighted by the group size distributions $d_s(n)$ and $d_a(n)$. Doing this, one has to consider separately the contribution of lonely individuals, who do not engage in a PGG, and whose payoffs are $-c$ for **S**s and 0 for **A**s.

The average payoff difference between **S**s and **A**s writes:

$$\begin{aligned} \Delta P(x) = & -c\, d_s(1) + \sum_{n \geq 2} \left[d_s(n) P_s(n) - d_a(n) P_a(n) \right] \\ = & -c + \sum_{n \geq 2} \frac{b\, d_s(n)}{n} + \sum_{n \geq 2} \frac{b}{n} \left[d_s(n) e_s(n) - d_a(n) e_a(n) \right] \end{aligned} \tag{2.3}$$

This formula is composed of three terms: the cost to the individual for its investment in a social action, which is payed also when the **S** player remains alone; the marginal gain for being social, averaged over groups of all sizes; and a third term combining the effect of within-group assortment to that of differential allocation in groups. While the second term necessarily declines when groups of larger size form in the population, the third term allows for different repartitions between groups (d_s and d_a) to compensate for unfavorable average interaction environment within groups of a given size. This compensatory effect may in principle even overcome negative within-group assortment (i.e. $e_a(n) > e_s(n)$).

When only one group size is present in the population, from eq. (2.3) one immediately retrieves the condition for the evolution of sociality found by Fletcher and Doebeli (2009). In case group formation is governed by an extreme recognition process leading **S**s to form groups only with their kind ($e_s(n) = n - 1$ and $e_a(n) = 0$ for all n), the condition $\Delta P(x) > 0$ reduces to $b/c > 1/(1 - d_s(1))$. Were no individual left alone, $b > c$ suffices in this case for sociality to evolve.

2.2.3 Payoff difference: case of no assortment *a priori*

When groups of different size are present, sociality can however thrive even in the absence of such within-group assortment, i.e. when $e_s(n) = e_a(n)$ for all $n \geq 2$. I refer to Appendix A for a treatment of the most general case (unspecified assortment). In the case of random within-group repartition, the interaction neighborhoods are equal:

$$e_s(n) = e_a(n) = (n-1)\, p(s|n) \tag{2.4}$$

with $p(s|n)$ the fraction of social players within groups of size n. Given the distributions $d_s(n)$ and $d_a(n)$, this equates to the quotient of the probability $d_s(n)\, x$ to pick a S individual that belongs to a group of size n and the probability $d_s(n)\, x + d_a(n)\,(1-x)$ to pick anyone (*S* or *A*) that belongs to a group of size n:

$$p(s|n) = \frac{d_s(n)\, x}{d_s(n)\, x + d_a(n)\,(1-x)} \tag{2.5}$$

Hence, eqs. (2.3), (2.4) and (2.5) yield:

$$\Delta P(x) = -c + \sum_{n=2}^{+\infty} \frac{b}{n} \left[(n-1) \frac{(d_s(n) - d_a(n))x}{(d_s(n) - d_a(n))x + d_a(n)} + 1 \right] d_s(n) \tag{2.6}$$

Note that the population composition x and the aggregation rules, which together determine the distributions d_s and d_a, are held fixed during group formation.

The fraction of **S** players will increase in the next generation whenever $\Delta P(x)$ is positive, and the evolutionary equilibria x_{eq} of the system are those such that $\Delta P(x_{eq}) = 0$. A condition for sociality to be favored when initially absent in the population writes $\Delta P(x = 0) > 0$ i.e. $b \sum_{n \geq 2} d_s(n)/n > c$. It is also the requirement for sociality to evolve when grouping tendencies are equal for both strategies ($d_s(n) = d_a(n) \; \forall \; n$) and can be interpreted as the condition for sociality to pertain to directly beneficial cooperation (see Box 2.2. of section 2.3.3). As illustrated by a toy model in the next section, sociality may be favored even when it is altruistic as soon as the distributions $d_a(n)$ and $d_s(n)$ experienced by the two strategies differ sufficiently. In the following, selection is assumed to be weak enough to guarantee a small change in frequencies from one generation to the next. The evolutionary dynamics is in this case approximated by a continuous-time replicator equation (Taylor and Jonker, 1978; Schuster and Sigmund, 1983; Hofbauer and Sigmund, 1998) (see Box 2.1.):

$$\dot{x} \propto x\,(1-x)\,\Delta P(x), \tag{2.7}$$

where the aggregation phase occurs infinitely fast with respect to evolutionary changes. If the time scales of aggregation and evolution were not separated, the evolutionary dynamics would be more correctly described by a discrete-time replicator equation that displays a potentially much more complex behavior (Villone et al., 2011).

Box 2.1. The replicator equation

The replicator equation is a fundamental equation to describe evolutionary dynamics with frequency-dependent selection. It was introduced by Taylor and Jonker (1978) (but see also Hofbauer and Sigmund (1998)). Let us consider n strategies that coexist in the population, and let us denote $\mathbf{x} = (x_1, \ldots, x_n)$ their respective frequencies (so that $\sum_{i=1}^{n} x_i = 1$). In its most common form, the replicator equation does not allow for mutations (but see below), so that a strategy that is missing initially remains absent. The general form can be written as a system of coupled differential equations as follows; for each $i = 1 \ldots n$,

$$\dot{x}_i = x_i \left(f_i(\mathbf{x}) - \bar{f}(\mathbf{x}) \right) \tag{2.8}$$

where $f_i(\mathbf{x})$ is the fitness of strategy i (that depends on the population state $\mathbf{x}$) and $\bar{f}(\mathbf{x}) = \sum_{i=1}^{n} x_i f_i(\mathbf{x})$ is the average population fitness. The interpretation is straightforward: the relative variation in evolutionary time $\dot{x}_i / x_i$ of the strategy i's frequency is obtained comparing its finess to that of the global population. The set S_n of the n-tuples $(x_1, \ldots, x_n)$ such that $\sum_{i=1}^{n} x_i = 1$, called *n-dimensional simplex*, is invariant under replicator dynamics, which ensures consistency with the biological interpretation. Each corner point of the simplex is an equilibrium (corresponding of a monomorphic population with one of the n strategies).

The replicator equation describes selection only, with neither drift nor mutation. It also relies on the hypothesis that the population is infinite (although there exists a discrete form, see for instance Villone et al. (2011)). In the case of two strategies **S** and **A** with respective frequencies x and $1 - x$ and average payoffs $P_S(x)$ and $P_A(x)$ examined here, the equation can be simplified as follows:

$$\begin{aligned} \dot{x} &\propto x \left[P_S(x) - (x P_S(x) + (1 - x) P_A(x)) \right] && (2.9) \\ &\propto x(1 - x) \left(P_S(x) - P_A(x) \right) && (2.10) \end{aligned}$$

(here, the "=" sign has been replaced by a proportionality sign "$\propto$" as we define fitnesses as linear rescaling of the game payoffs). Therefore, $x = 0$ and $x = 1$ are two absorbing equilibria of the dynamics, and every other equilibrium x_{eq} must satisfy $P_S(x_{eq}) = P_A(x_{eq})$.

The replicator equation can also be generalized to include mutations, e.g. in a two-strategy case

$$\dot{x} = [x(1-u) + (1-x)u]\, f_1(x) - x\bar{f}(x) \tag{2.11}$$

where u is the mutation rate between strategy 1 and strategy 2.

The next section illustrates these conclusions by a toy model with an explicit mechanism of aggregation underpinning different group size distributions for the two strategies. This mechanism is chosen such that it creates no assortment *a priori*. The equations derived in this section can then be applied to study the evolutionary dynamics of the social strategy along with that of the group size distributions.

2.3 Group formation by differential attachment

2.3.1 Description of the toy model

In this section, I apply the former results to an illustrative model where group formation is based on simple hypotheses regarding individual interactions. I explain how social behavior characterized by an increase in individual "stickiness" might evolve, and clarify the mechanism giving rise to assortment at the population level even in the absence of peer recognition. **S** individuals produce a costly glue that increases their chances to attach to any individual they come in contact with. At the same time, it enhances overall group cohesion to a higher extent than an **A** individual more loosely glued to its group. This is consistent with the assumption that sociality entails differences both in the process of group formation, and in the contribution to group welfare. The following scheme for group formation is deliberately crude so as to remain analytically tractable and make the conditions for evolution of social attachment explicit. It should nonetheless be taken as a proof of principle that a social behavior can evolve via a biologically plausible mechanism of blind interactions among unrelated individuals, where assortment is an emergent property of the group formation process.

This model reflects some features of social microbes that are able to produce adhesive proteins at their surface. Although in some cases adhesion proteins are strain-specific and allow to recognize other bearers by direct matching, one can imagine that, in the early stages of social evolution, cells might have been endowed with generic adhesion-enhancing properties. In this case, stickiness can be regarded as an *a priori* property of a subpopulation of cells, that is energetically costly and entrains higher group-level productivity (e.g. in the search for prey, protection against predators, dispersal efficiency, etc.) since aggregates composed of a higher proportion of adhesive cells are more cohesive.

More specifically, this model mirrors the properties of, for instance, social amoebas and bacteria. These microbes are thought to possess inheritable social strategies, whereby cells have different propensities to sacrifice for others, participating to the construction of the stalk of a fruiting body rather than becoming spores. The success of the genes that are passed on to the following generation is determined by the composition of the spore pool in all the groups (fruiting bodies) that are formed within the population at the aggregation stage of the life cycle. Enhanced probabilities to end up in the stalk are moreover often found associated to a higher stickiness (Strassmann and Queller, 2011).

Let us consider an infinite population composed of a fraction x of **S** and a fraction $(1-x)$ of **A** individuals that differ in their attachment abilities. At each generation, aggregates form from patches of T individuals that are randomly drawn from the population pool. Group formation in each patch is nucleated by one individual, named *recruiter*, that is chosen at random within the set. The remaining $(T-1)$ individuals are sequentially given one possibility to attach to the recruiter and hence to join the group. This one-shot adhesion step leaves some players outside the groups. Such lonely individuals are commonly observed in microorganisms (see for instance Smukalla et al. (2008); Dubravcic et al. (submitted)) and will play an important role in the emergence of sociality in this model. Attachment probabilities are fixed for any couple of strategies: between two **S** (resp. an **S** and an **A** individual; two **A**) individuals, it is denoted by π_{ss} (resp. $\pi_{as}; \pi_{aa}$).

S individuals attach more efficiently, so that $\pi_{ss} \geq \pi_{as} \geq \pi_{aa}$. Moreover, we choose these probabilities such that no preferential interactions favor assortment between **S** players. This hypothesis reflects the requirement that interactions are not assortative *a priori*, unlike when social individuals recognize and select groups that are composed of a larger fraction of their kind. For a given composition of the population, it means that, among the individuals you attach to in dyadic interactions, the expected proportion of **S**s does not depend on your type. For an **S** (resp. **A**) focal player, the probability to attach to a random individual is $x\pi_{ss} + (1-x)\pi_{as}$ (resp. $x\pi_{as} + (1-x)\pi_{aa}$), and the probability to attach to a **S** is $x\pi_{ss}$ (resp. $x\pi_{as}$), so that the former condition becomes

$$\frac{x\pi_{ss}}{x\pi_{ss} + (1-x)\pi_{as}} = \frac{x\pi_{as}}{x\pi_{as} + (1-x)\pi_{aa}}, \tag{2.12}$$

that is fulfilled for every x provided

$$\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}} \tag{2.13}$$

This condition is consistent with that found by Taylor and Nowak (2006). When $\pi_{as} \leq \sqrt{\pi_{ss}\pi_{aa}}$, the expected proportion of **S** co-players is higher for **S** than for **A** individuals, i.e. positive assortment among **S** would occur if the interactions were only pairwise. On the other hand, $\pi_{as} \geq \sqrt{\pi_{ss}\pi_{aa}}$ would denote prior negative assortment in a dyadic context. In the analytical calculation, attachment probabilities will be chosen so as to satisfy eq. (2.13), but this assumption will be relaxed in section 2.3.4 and rules of attachment generating non-null prior assortment will be considered.

2.3.2 Group size distributions and payoff difference

In Appendix B, I derive analytically the size distributions for the **S** and **A** types, given the previously described mechanism for group formation. These distributions are illustrated in Fig. B.1. They are the superposition of a component in $n = 1$ (players remaining alone) and of two binomial distributions of respective averages $T\left[x\pi_{ss} + (1-x)\pi_{as}\right]$ and $T\left[x\pi_{as} + (1-x)\pi_{aa}\right]$, corresponding to group nucleated by **S** (resp. **A**) recruiters. Their relative weights depend on the social type: **S**s are less often alone than **A**s. Increasing the fraction of **S**s, the two nonsingular distributions shift toward higher group sizes.

Knowing the group size distributions emerging from the aggregation process, the payoff difference $\Delta P(x)$ can be computed for a given composition of the population. Figure 2.2 shows such payoff difference obtained by substituting eqs. (B.1) and (B.2) of Appendix B in eq. (2.6). $\Delta P(x)$ is displayed for different values of the game parameters b and c and the aggregation parameters π_{ss}, π_{aa} and T. The advantage of social over asocial players increases monotonically with x, and is zero at most at one (unstable) equilibrium x^*.

2.3.3 Evolutionary dynamics and effect of the parameters

The internal equilibrium x^* exists in a large region of the parameters space. In this region, the evolutionary dynamics ruled by the replicator equation (2.7) is bistable, with two additional stable monomorphic equilibria of full asociality $x = 0$ and full sociality $x = 1$. Sociality invades as soon as x is larger than the threshold value x^*. Once established, full sociality is stable against the invasion by **A**s. This scenario is qualitatively different from the case of one single group size, where the evolutionary dynamics can only lead to full asociality for linear PGGs.

Figure 2.3 displays the coupled dynamics of the social strategy and of the group size distributions in a numerical simulation of a large population. Initially, only **A**s are present in the population, and the threshold is reached thanks to random mutations. As the frequency of **S**s

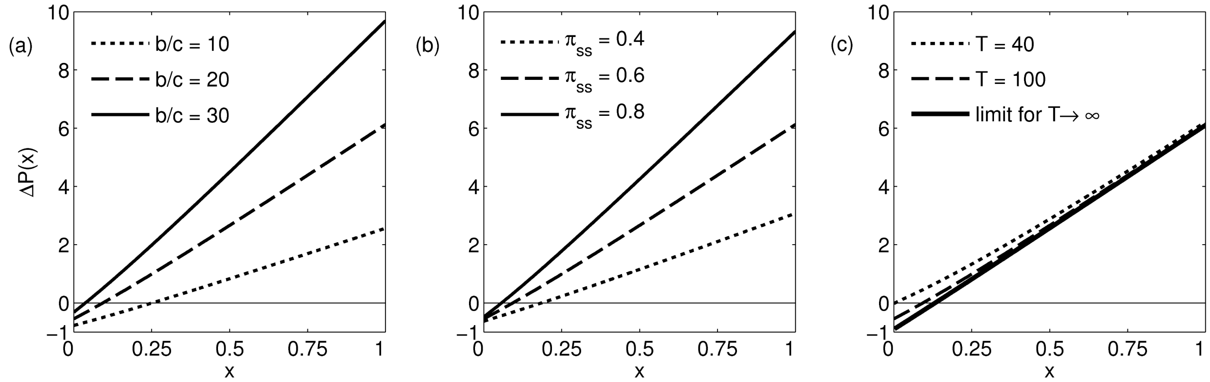

Figure 2.2: Payoff difference changing one parameter at a time

Average payoff difference between **S** and **A** individuals as a function of the frequency x of **S**s as one parameter is changed: (a) the benefit-to-cost ratio b/c, with $\pi_{ss} = 0.6$, $\pi_{aa} = 0.1$, $T = 100$; (b) the social-to-social attachment probability π_{ss}, with $\pi_{aa} = 0.1$, $b/c = 20$, $T = 100$; (c) the upper bound for group size T, with $\pi_{ss} = 0.6$, $\pi_a = 0.1$, $b/c = 20$. In each case $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$. Sociality evolves and invades the population as soon as it reaches a threshold frequency x^*. Invasion by the social strategy is facilitated by either a large benefit-to-cost ratio, a high adhesiveness or smaller maximal group sizes. However, there exists a threshold x^*_∞ above which sociality evolves for any maximal group size (panel c).

increases, groups of progressively larger size form and concomitantly the fraction of lonely individuals decreases. The difference between the distributions for **S**s and **A**s is enhanced by the fact that the balance between the solo and group components of these distributions is affected in opposite directions by the evolutionary dynamics.

When all players are social, a fraction $1 - \pi_{ss}$ of individuals remains alone, while the others belong to groups binomially distributed around an average size $T\pi_{ss}$. Notice that the group size at the social equilibrium is not influenced by the parameters b and c defining the public goods game, but only by parameters determining the group formation process. In particular, the average group size arising in fully social populations linearly depends on the maximal possible group size T.

Figure 2.4 recapitulates the evolutionary dynamics by displaying the threshold frequency x^* for sociality to invade.

Figure 2.4a confirms that sociality evolves more easily the bigger the difference between **S**

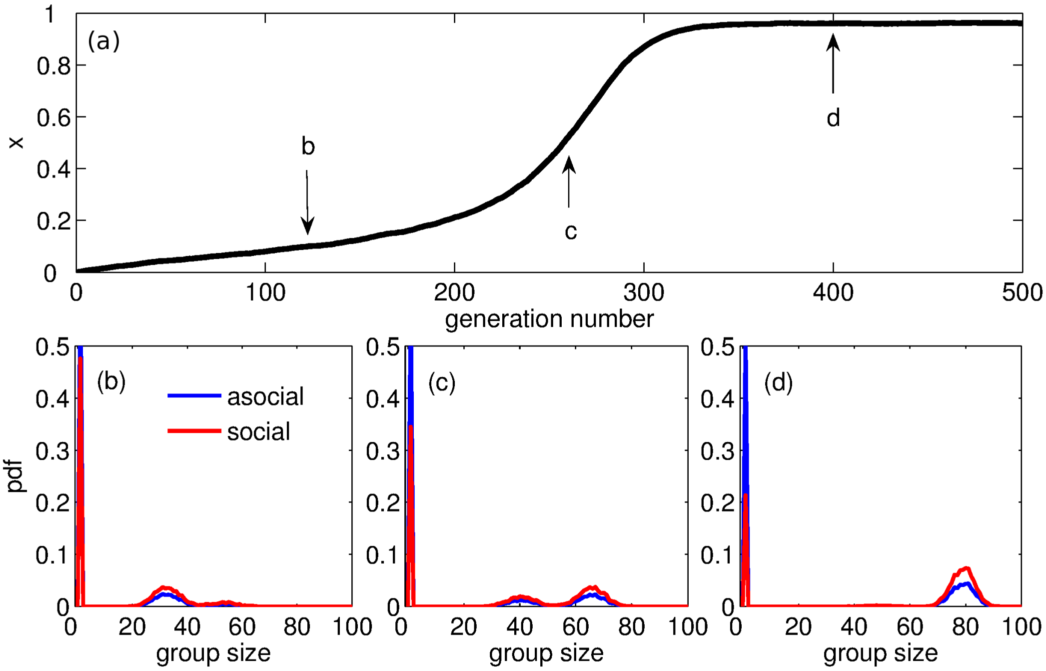

Figure 2.3: Evolutionary trajectory and group size dynamics

One run of the evolutionary algorithm, starting from a population of **A** individuals with random mutations on newborns, with rate $u = 0.01$. (a) time evolution of the frequency x of the social type. (b-d) snapshots at generation 120 (b), 260 (c) and 400 (d), indicated by the arrows in panel (a), of the group size distributions experienced by **S** (red) and **A** (blue) individuals. The social trait rises towards fixation in the population while distributions displace towards larger group sizes. Parameters: $\pi_{ss} = 0.8$, $\pi_{aa} = 0.3$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $b/c = 20$, $T = 100$, carrying capacity $= 10^6$, $x(0) = 0$, $f_{max} = 0.5$, $f_{min} = 0.1$.

and **A** individuals' attachment probabilities. Figure 2.4b shows that the threshold frequency x^* decreases, as one would expect, as b/c increases. The threshold x^* increases with T, consistently with the common claim that the evolution of altruism is easier in small groups (Olson, 1971). However, when $T \to +\infty$, it converges to a value $x^* < 1$ (Figure 2.2c), meaning that there exist a critical initial frequency of **S**s such that sociality will invade whatever is the maximal group size. Although higher cooperation levels are believed to occur more easily in small groups, group formation by differential attachment thus does not impose an *a priori* burden on large groups. This suggests that unsophisticated interaction rules may be relevant in explaining how sociality is maintained in the microbial world, where social aggregates are commonly composed of a large

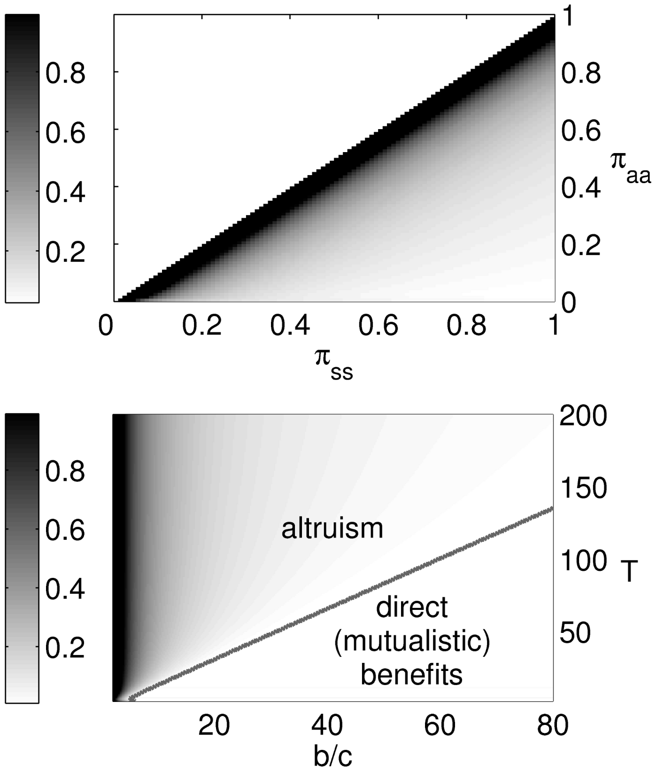

Figure 2.4: Social invasion thresholds

Threshold frequency x^* of social individuals required to trigger the evolution of sociality through the replicator equation: (a) x^* as a function of adhesiveness π_{ss} and π_{aa} (with $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $b/c = 20, T = 100$); (b) x^* as a function of b/c and T ($\pi_{ss} = 0.6$, $\pi_{aa} = 0.2$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$). For values of b/c below the grey line, the evolution of cooperative sociality is trivial, corresponding to direct benefits, whereas above the line it is altruistic.

number of cells, e.g. thousands of them in flocculating yeast (Smukalla et al., 2008), or up to 10^5 in *D. discoideum* (Tang et al., 2002).

The fact that x^* is always positive means that, in general, an infinitesimal initial load of **S**s, as is generated by extremely rare random mutations, is not sufficient for sociality to evolve in the first place. However, when the threshold is low, numerous mechanisms can lead the frequency of the social strategy over the threshold, e.g. random fluctuations due to finite-size effects, non-infinitesimal mutation rates or incomplete reshuffling from one generation to the next. Numerical simulations show that, in finite populations subject to a small mutation rate, the evolution of

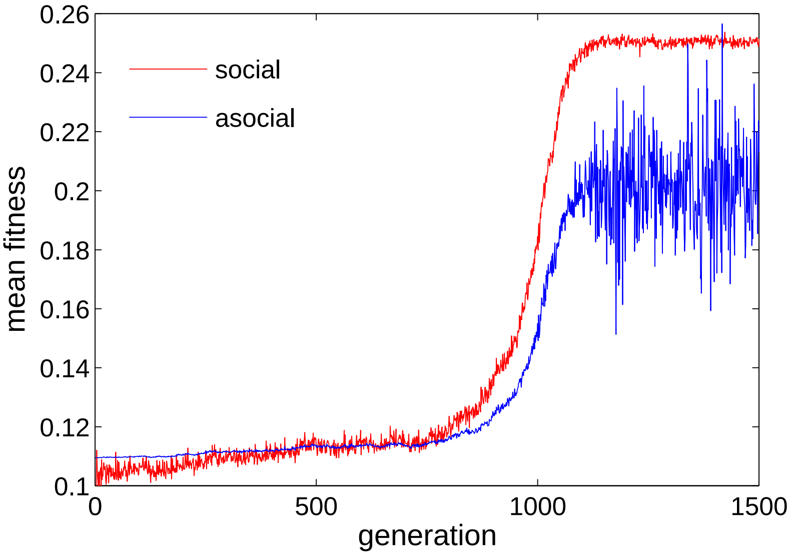

Figure 2.5: Mean fitnesses of the **S** and **A** strategies when **S**s invade from scratch in a small population ($N_{pop} = 1000$)

Initially, **S**s (red) are outcompeted by **A**s (blue) and thus cannot rise in frequency. However, the constant mutation load keeps sociality away from extinction. When some of the few **S**s happen to accrue larger payoffs than the average **A** player by chance, social frequency might reach the invasion threshold and fixate in the population.

sociality is indeed easier than analytically expected (Fig. 2.5)

The region where sociality is evolutionary stable is larger than the region where the social behavior implies direct benefits, i.e. when the marginal gain of a social individual is larger than c (Wilson, 1979; Pepper, 2000). See Box 2.2. for the definition and calculation of the condition that delimits such region where sociality trivially evolves. Figure 2.4 shows that sociality evolves and is maintained in the population for a wide range of nontrivial parameters, i.e. even when it is an essentially altruistic act right at its onset.

Box 2.2. Condition for sociality to be altruistic

In the case of a Public Goods Game played in a group of fixed size N, cooperation can evolve if and only if the marginal benefit from one's own cooperation b/N is large enough to compensate the investment c, that is when $b/c > N$. Nontrivial cases, where additional assumptions are required for cooperation to evolve, are thus characterized by the condition:

$$\frac{b}{c} < N. \tag{2.14}$$

To generalize this condition when group size is no longer fixed but stems from an aggregation process, the marginal benefits b/n needs to be averaged over all group sizes $n \geq 2$. As **S**s experience a group size distribution $d_s(n)$, the condition for altruism reads:

$$\sum_{n\geq 2} \frac{b}{n} d_s(n) - c < 0$$

i.e.

$$\frac{b}{c} < \frac{1}{\sum\limits_{n\geq 2} \frac{d_s(n)}{n}} := r_{alt}(x) \tag{2.15}$$

In the case of group formation by differential attachment, the critical benefit-to-cost ratio r_{alt} can be calculated from the analytical expressions of the distribution d_s of **S**s' experienced group size. This calculation is performed in Appendix C.

2.3.4 Other rules for group formation

So far, it was assumed that players undergo blind interactions whereby individuals attach, according to their strategies, with probabilities π_{aa}, π_{as} and π_{ss} in geometric progression, ensuring no *a priori* assortment. However, other formulations of the adhesion probability, reflecting different settings of pairwise interactions, can be contemplated, and will in general result in nonrandom assortment within groups of a given size. In these cases, eq. (2.6) does not hold any longer, but the payoff difference can anyway be numerically computed by repeatedly simulating the aggregation process.

Figure 2.6 displays the difference in payoff between **S**s and **A**s for the two cases where the attachment probabilities take up their extreme values: $\pi_{as} = \pi_{ss}$ and $\pi_{as} = \pi_{aa}$. In these model configurations, it is the **S** (resp. **A**) co-player that takes the lead in deciding the outcome of binary interactions. The first rule, where the **A**-**S** attachment probability is maximal, reduces the threshold for sociality to spread in the population. At the same time, the fully social equilibrium is destabilized: when chances to encounter a **S** are high, sociality becomes a "wasted investment" and asociality is favored again. The resulting evolutionarily stable equilibrium is polymorphic: **S**s and **A**s coexist. In contrast, when the **A**-**S** attachment probability is minimal, the invasion barrier x^* is more difficult to reach compared with null *a priori* assortment. However, the fact that asocials are more efficiently segregated when the population is largely social, makes the fully social equilibrium even more stable with respect to larger attachment probabilities. Any other choice for π_{as} such that $\pi_{aa} \leq \pi_{as} \leq \pi_{ss}$ leads to thresholds x^* between those two extremal values. Therefore, the potential for social behavior to become stable in the population is not challenged by the amount of *a priori* assortment generated by the attachment rules.

2.4 Decoupling cooperation and attachment

2.4.1 Hypotheses

Previously, individuals had a fixed strategy during the whole life cycle. Let us now consider that they may change their phenotype between the aggregation phase and the in-group phase, for instance that initially aggregative players may refrain from contributing to group cohesion during the game (e.g. by turning off glue production). Such a strategy would correspond to perfect free-riding, as players do not pay the cost of cooperation during the in-group phase but still get the potentially enhanced gains of sociality. However, one can imagine that the ability to "switch" their phenotype entails an additional regulation cost. Four strategies are thus defined: 1) sticky-

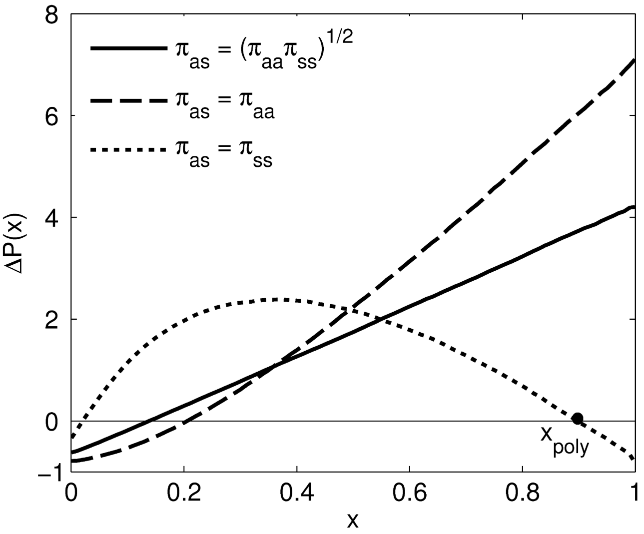

Figure 2.6: Payoff differences for other rules of attachment

Payoff differences between **S**s and **A**s obtained by simulation of the group formation process, for different rules of attachment: $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, corresponding to null within-group assortment (full line); $\pi_{as} = \min(\pi_{ss}, \pi_{aa}) = \pi_{aa}$, corresponding to positive prior assortment (dashed line); $\pi_{as} = \max(\pi_{ss}, \pi_{aa}) = \pi_{ss}$, corresponding to negative prior assortment (dotted line). Parameters values: $\pi_{ss} = 0.6$, $\pi_{aa} = 0.2$, $b/c = 20$, $T = 100$. For the third rule of interaction, the threshold x^* to trigger the evolution of sociality decreases, but sociality does not invade fully and is only profitable up to a frequency x_{poly} where the population attains a polymorphic equilibrium.

cooperators (**SC**) that are aggregation-prone and sustain group cohesion, thus paying the whole cost $-c$; 2) nonsticky-cooperators (**AC**), i.e. asocial individiduals that become adhesive only for the reproductive phase, therefore paying only a part αc of the cost ($0 \leq \alpha \leq 1$); 3) sticky-defectors (**SD**), or "cheaters", that are adhesive while they aggregate but refrain from being so afterwards, therefore paying only the complementary part $(1 - \alpha)c$ of the cost; 4) nonsticky-defectors (**AD**), who pay nothing. Parameter α can be understood as, for instance, the duration of the in-group phase normalized to that of the whole life cycle: if $\alpha = 0$, the cost of adhesion mainly relates to the aggregation phase; if $\alpha = 1$, it mainly relates to the grouped phase. In addition, the "switching strategies" (i.e. **SD** and **AC**) pay a cost C_s.

Let us define x, y, z the frequencies of, respectively, strategies **SC**, **AC**, **SD** (so that $1 - x - y - z$ is the frequency of strategy **AD**). The aggregation process used here is the same as in the toy model of the previous section, so that the distribution $d_{S\bullet}(n)$ (resp. $d_{A\bullet}(n)$) experienced by the two sticky strategies **SC** and **SD** (resp. the two nonsticky strategies **AC** and **AD**) is the same as $d_S(n)$ (resp. $d_A(n)$) in the former section, substituting x by the total proportion of sticky individuals $x+z$ (resp. substituting $1-x$ by the total proportion of nonsticky individuals $1-x-z$).

Mean payoffs can also be calculated similarly as before:

$$P_{SC} = b \sum_{n \geq 2} \frac{d_{S\bullet}(n)}{n} \left[\frac{x\, d_{S\bullet}(n) + y\, d_{A\bullet}(n)}{(x+z) d_{S\bullet}(n) + (1-x-z) d_{A\bullet}(n)} + 1 \right] - c \tag{2.16}$$

$$P_{AC} = b \sum_{n \geq 2} \frac{d_{A\bullet}(n)}{n} \left[\frac{x\, d_{S\bullet}(n) + y\, d_{A\bullet}(n)}{(x+z) d_{S\bullet}(n) + (1-x-z) d_{A\bullet}(n)} + 1 \right] - \alpha\, c - C_s \tag{2.17}$$

$$P_{SD} = b \sum_{n \geq 2} \frac{d_{S\bullet}(n)}{n} \left[\frac{x\, d_{S\bullet}(n) + y\, d_{A\bullet}(n)}{(x+z) d_{S\bullet}(n) + (1-x-z) d_{A\bullet}(n)} \right] - (1-\alpha)\, c - C_s \tag{2.18}$$

$$P_{AD} = b \sum_{n \geq 2} \frac{d_{A\bullet}(n)}{n} \left[\frac{x\, d_{S\bullet}(n) + y\, d_{A\bullet}(n)}{(x+z) d_{S\bullet}(n) + (1-x-z) d_{A\bullet}(n)} \right] \tag{2.19}$$

2.4.2 Evolutionary outcome

Knowing the mean payoffs, evolutionary trajectories can be computed using the replicator equation. Figure 2.7 displays the evolutionary endpoints for a given set of parameters and an initial population with 25% of each strategy, as a function of the parameter α and the switching cost C_s. The frequency of each strategy is represented at equilibrium for $c = 1$.

In most cases, the equilibrium is monomorphic. The results may be somewhat tricky to interprete, as in mixed populations each strategy affects the three others. They can however be crudely understood as follows (readers in a hurry can jump to the conclusion in section 2.4.3):

- For $\alpha \simeq 0$, **SD**s are disavantaged compared to **SC**s as the former actually pay a larger cost ($\simeq 1 + C_s$) than the latter ($= 1$), and do not get direct benefits. They disappear quickly and **SC**s tend to get assorted positively with the remaining other sticky players that are thus all cooperators too. As **AC**s tend to get assorted positively with other nonsticky players,

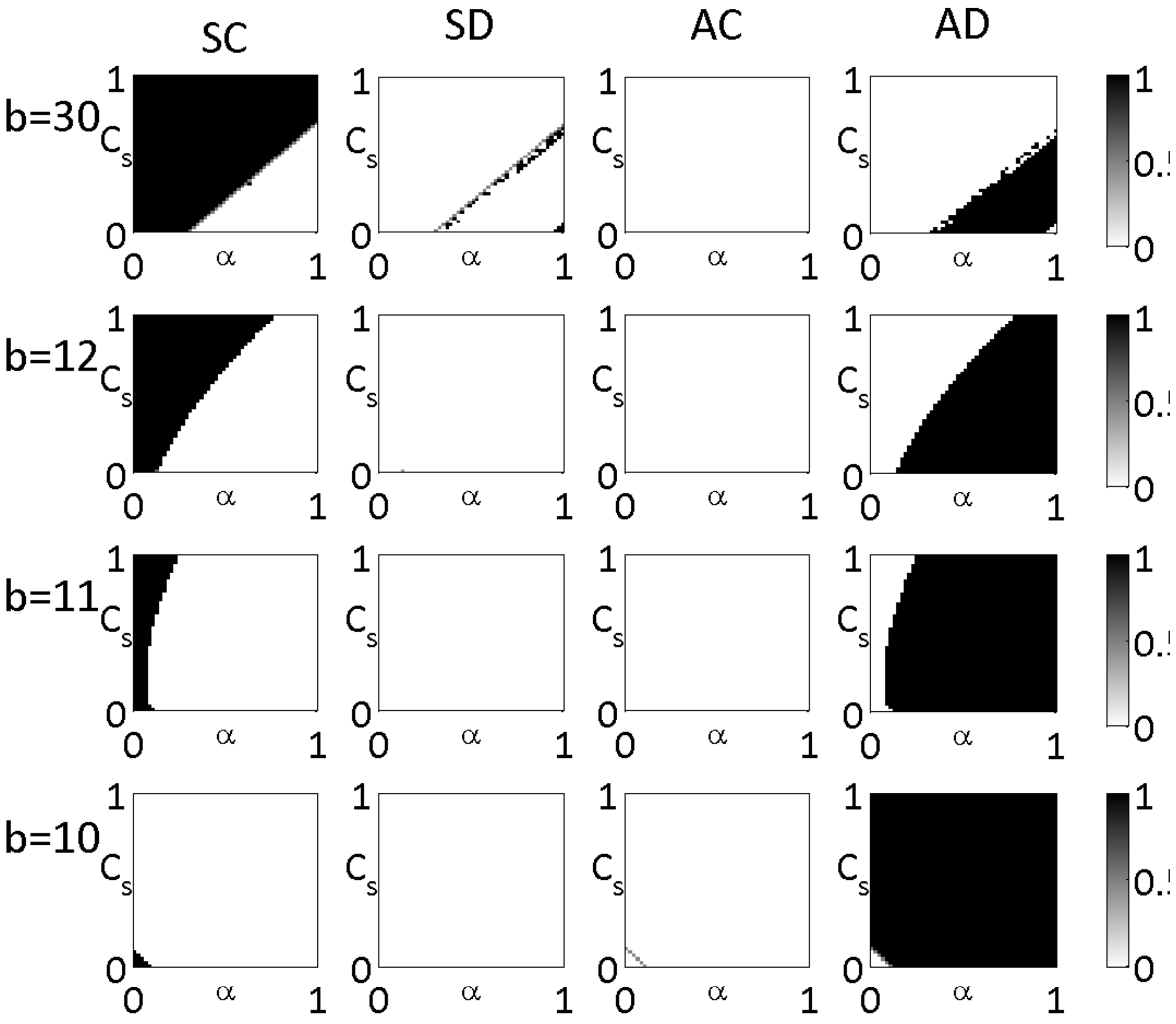

Figure 2.7: Equilibrium frequencies of each strategy **SC**, **SD**, **AC**, **AD** when sociality is decoupled from cooperation.

Frequencies range from 0 (white) to 1 (black). Equilibrium frequencies are represented for a different benefit-to-cost ratio b/c in each line. In most cases, the equilibrium population is either fully **SC** or fully **AD**. High values of C_s and low values α of favor the **SC** strategy. For a few combinations of parameters C_s and α, the **SD** strategy can take over (here when $b = 30$) or co-exist at equilibrium with the **SC** strategy (here when $b = 30$, gray line). Parameters: $x_0 = y_0 = z_0 = 0.25$, $c = 1$, $C_s = 0.44$, $\alpha = 0.74$, $\pi_{ss} = 0.6$, $\pi_{aa} = 0.3$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $T = 100$.

among whom **AD**s, they experience less cooperative groups and are outcompeted by **SC**s. Cooperation levels in nonsticky players' average groups decrease and **AD**s, even though they pay no cost, are themselves defeated by **SC**s that belong to highly cooperative groups. As a result, **SC**s take over.

- Let us consider now intermediate to large α. When C_s is high, **SD**s pay a cost $(1-\alpha)+C_s$ that tends to outgrow the fixed cost 1 of **SC**s, and are again defeated by them as they experience the same groups and get no direct benefits, unlike **SC**s. Similarly to the case of low α, **SC**s thrive as they get assorted in highly cooperative (thus profitable) groups, unlike the two nonsticky strategies.

  When C_s decreases however, the cost payed by **SD**s gets smaller than the cost payed by **SC**s. When the nonsticky strategies are eliminated successively (first **AC**s, as they pay too high a cost to rival the sticky strategies, then **AD**s, as they get assorted with mainly nonsticky, and now defective, individuals), the direct benefit $b\sum_{n\geq 2} d_{S\bullet}(n, x+z=1)/n$ earned by **SC**s is constant. **SC**s and **SD**s experience the same average groups, so that at some point, the cost $1-\alpha+C_s$ payed by **SD**s might compensate exactly the (cost + direct benefit) $1+b\sum_{n\geq 2} d_{S\bullet}(n, x+z=1)/n$ of the **SC**s. This results in a mixed equilibrium of **SC**s and **SD**s (e.g., for $b=30$, the gray diagonal of equation $C_s = \alpha - b\sum_{n\geq 2} d_{S\bullet}(n, x+z=1)/n$ in Figure 2.7), as both strategies have the same mean payoffs. Other initial frequencies lead to different mixtures of **SC**s and **SD**s (Fig. 2.8), as all of them are stable. It is however a non-generic situation.

  When C_s is decreased further, **SD**s outcompete **SC**s and get assorted among other sticky players, that are now mainly defectors. **SD**s thus get poor payoffs from their groups and are defeated by the nonsticky strategies. **AD**s finally take over, as they do not pay any cost unlike **AC**s.

When the benefit-to-cost ratio decreases, the parameters range where the population end up

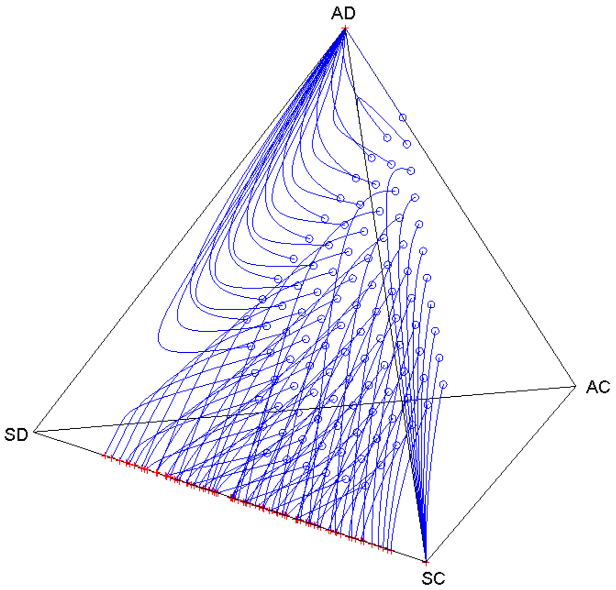

Figure 2.8: A non-generic case of evolutionary trajectories in the 3D-simplex for various initial conditions.

Evolutionary trajectories start setting initial frequencies of each strategies represented by blue circles and end at equilibrium frequencies represented by red crosses. Apart from the full-**SC** and full-**AD** monomorphic equilibria, any mixed equilibrium with **SC**s and **SD**s is stable. This results from average payoffs P_{SC} and P_{SD} being equal (with the chosen costs) when asocial strategies **AC** and **AD** are eliminated in the population. Parameters: $b = 30$, $c = 1$, $C_s = 0.44$, $\alpha = 0.74$, $\pi_{ss} = 0.6$, $\pi_{aa} = 0.3$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $T = 100$. Parameters C_s and α are chosen such that $C_s = \alpha c - b\sum_{n\geq 2} d_{S\bullet}(n, x+z=1)$ (on the grey line in the first line of Figure 2.7)

.

being fully **SC** shrinks, as cooperation becomes less profitable.

2.4.3 Conclusion

An interesting feature of this model is that in most cases, either **SC**s or **AD**s take over the population: only in very rare situations do the “switching strategies” **SD** and **AC** persist. This tends to legitimate *a posteriori* the assumption made formerly that sociality (or stickiness) and cooperation can be regarded as coupled.

2.5 Extension to a continuous trait

In some cases, social propensity can result from individual features that do not abide by an binary logic (a tunable motility or adhesion force, etc.) For instance, the FLO1 gene governing adhesion in yeast is highly variable: the level of adhesion indeed changes as a function of the number of tandem repeats within FLO1 (Smukalla et al., 2008). It may then be instructive to check whether the mechanism described above still hold for mutations that affects continuously an individual's social inclination.

2.5.1 Changes in the model

Let us assume the existence of a social trait z that can take any value in the interval $[0, 1]$. $z = 1$ means the individual is "fully social", $z = 0$ that he is "fully asocial". The associated cost $c(z)$ is an increasing function of z. In the following, I will assume it linear ($c(z) = -Cz$), but keep in mind that nonlinear functions can diversify possible dynamics: e.g. in (Doebeli et al., 2004), quadratic cost functions lead to a branching process used to explain the origin of cooperators with a fixed contribution. Individuals assemble into groups according to some rules. This analysis only considers the case of a rare mutant characterized by z in a monomorphic population characterized by a sociality $\hat{z}$. The question is whether a rare mutant trait z can invade or not a resident monomorphic population characterized by $\hat{z}$. Accordingly to the adaptive dynamics formalism (Geritz et al., 1998; Waxman and Gavrilets, 2005), it is assumed that 1) the mutation rate is small enough so that the population has time to reach its equilibrium before another mutation occurs; 2) mutations are infinitesimal. Those classical hypotheses, however strong as they may seem, are necessary to circumvent some untractable calculatory issues and still shed light on which dynamics are to be expected (see Box 2.3.). Group size distributions experienced by an individual depend on the z-values of others as well as its own: for a z-mutant in a $\hat{z}$-population, it is denoted $g(n, z, \hat{z})$; for a resident individual, $g(n, \hat{z}, \hat{z})$. Unless she is alone, the group-related payoff derived by an individual is $b\bar{z}$, where $\bar{z}$ is the mean value of the group members' traits.

Box 2.3. The adaptive dynamics framework

Adaptive dynamics is a methodological tool formalized by Geritz et al. (1998) and aimed at describing the long-term phenotypic changes that result from small mutations on a specific gene in an evolving population (see also Waxman and Gavrilets (2005) for a very clear tutorial). Let us consider a population characterized by a single, continuously varying phenotypic trait. Adaptive dynamics relies on several (somewhat unrealistic) assumptions, namely:

- that each mutation cause infinitesimal phenotypic change;
- that the ecological time scale is much quicker than the evolutionary time scale, to such extent that before a novel mutation arises, the population has time to stabilize to a monomorphic state;
- that the success of a mutant trait in replacing or not the resident trait in the population depends on its growth rate when it is still infinitely rare in the population.

Let then r be the resident value of the trait at some point in time. We need to assess whether it can be outcompeted by a small mutation m. We thus calculate the *invasion fitness* (i.e. the relative growth rate when rare) $S(m, r) - S(r, r) = S(m, r)$ of the mutant in a full-r population (here $S(r, r)$ is set to 0 due to the population being at a dynamical equilibrium). As mutation are small, the linear approximation $S(m, r) \simeq \left[\partial S(m, r)/\partial m\right]_{m=r} (m - r)$ is valid and the fate of the mutant can be determined by the sign of the selection gradient $\left[\partial S(m, r)/\partial m\right]_{m=r}$. If the selection gradient is $= 0$ for values $r = r^*$, then the fitness landscape is flat near r^*. Such particular values are called *evolutionary singular strategies*. If it is positive (resp. negative), then mutants with larger (smaller) phenotypic values than the resident population's invade.

Adaptive dynamics is particularly useful as it enables to characterize the equilibria or singular strategies more thoroughly than standard evolutionary game theory. This can be done calculating the second derivatives or the invasion fitness (not detailed here). Singular strategies can be classified according to four criteria:

1. its non-invasibility: the singular strategy is an *evolutionarily singular strategy* (ESS) whenever a resident r^*-population cannot be invaded by any nearby mutant. This is a local version of the usual ESS condition;
2. the ability for r^*-mutants to invade a resident population with phenotype r close to, but not equal to r^*;
3. its *convergence-stability*, i.e. whether it can actually be reached by a succession of mutations. It happens whenever a r-population, with r close to, but not equal to r^*, is invaded only by mutants that lie even closer to r^*;
4. whether or not two neighboring phenotypes lying either side of r^* can invade each other; in this case, there exists a protected polymorphism of traits at both sides of r^*.

A compelling way to summarize all this information is the *pairwise invasibility plot* (PIP), that is built plotting the line $m = r$ (along which mutants and residents have the same phenotype, and the invasion fitness is 0) and the sign of the invasion fitness for each (m, r) combination (Fig. 2.9A). The singular points (if any) lie where the curve $S(m, r) = 0$ and the line $m = r$ intersect. According to the shape of the PIP around a singular phenotype (eight different configurations exist, as shown on Figure 2.9B), the nature of the equilibrium (relative to the four criteria presented above) can be inferred.

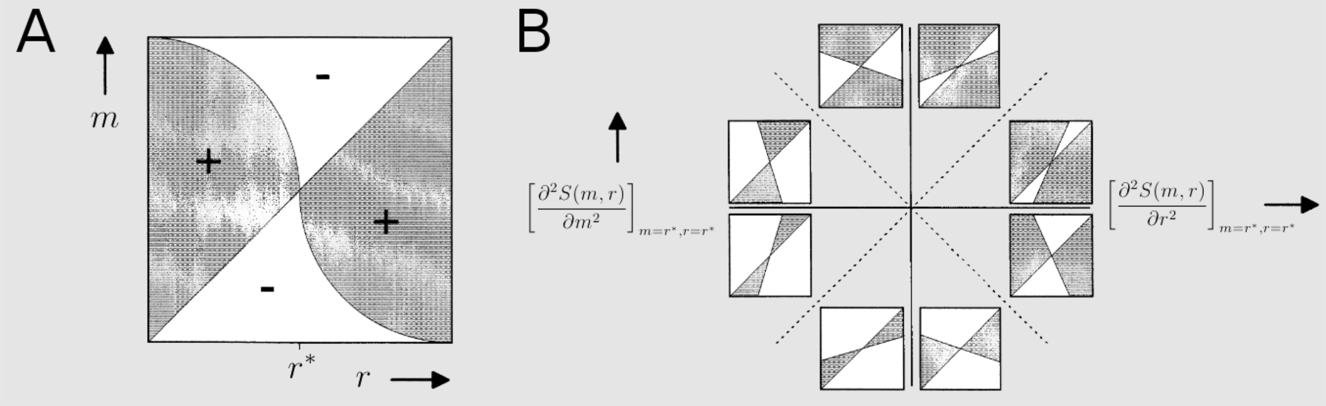

Figure 2.9: Pairwise invasibility plots (PIP)

Panel A: example of a PIP. The gray (resp. white) areas are those where the invasion fitness is positive (resp. negative); r^* is an evolutionary singular strategy. The shape of the PIP near (r^*, r^*) enables to characterize the equilibrium. Panel B: the eight configurations for a singular strategy. The shape of the PIP near the singular strategy is determined by the algebraic value of second derivatives of the invasion fitness. According to these values, one can determine which of the four properties of the equilibrium presented above are satisfied and infer the evolutionary dynamics. Adapted from Geritz et al. (1998).

2.5.2 Resident / mutant analysis

In a given group of size n, a resident individual gets a payoff

$$P_n(\hat{z}, \hat{z}) = b\,\hat{z} \tag{2.20}$$

as $\bar{z} = \hat{z}$; whereas, for a z-mutant,

$$P_n(z, \hat{z}) = b\,[(n-1)\hat{z} + z]\,/\,n = b\,\hat{z} + b\,(z - \hat{z})/n \tag{2.21}$$

Let us call $u(\hat{z}, \hat{z})$ (resp. $u(z, \hat{z})$) the proportion of $\hat{z}$-individuals (resp. z-individuals) left ungrouped ($u(\hat{z}, \hat{z}) = g(1, \hat{z}, \hat{z})$ and $u(z, \hat{z}) = g(1, z, \hat{z})$). Weigthing for any possible group size, the final net payoff of the resident trait is:

$$P(\hat{z},\hat{z}) = \sum_{n\geq 2} g(n,\hat{z},\hat{z})\, P_n(\hat{z},\hat{z}) - c(\hat{z}) \tag{2.22}$$

$$= b\,\hat{z}\,[1-u(\hat{z},\hat{z})] - C\hat{z} \tag{2.23}$$

and, for a mutant,

$$P(z,\hat{z}) = \sum_{n\geq 2} g(n,z,\hat{z})\, P_n(z,\hat{z}) - c(z) \tag{2.24}$$

$$= b\,\hat{z}\,(1-u(z,\hat{z})) + b(z-\hat{z})\sum_{n\geq 2} g(n,z,\hat{z})/n - Cz \tag{2.25}$$

The mutants being at very small frequency by assumption, the average payoff in the population $\bar{P} \approx P(\hat{z},\hat{z})$; therefore, the relative growth rate of the mutant trait is:

$$S(z,\hat{z}) = P(z,\hat{z}) - P(\hat{z},\hat{z}) \tag{2.26}$$

$$= b\,\hat{z}\,[u(\hat{z},\hat{z}) - u(z,\hat{z})] + b(z-\hat{z})\sum_{n\geq 2} g(n,z,\hat{z})/n - C(z-\hat{z}) \tag{2.27}$$

and that of a resident, $S(\hat{z},\hat{z}) = 0$.

Now, let us calculate the fitness gradient of the $\hat{z}$-resident, supposing that all relevant functions are differentiable:

$$\left.\frac{dS(z,\hat{z})}{dz}\right|_{z=\hat{z}} = \lim_{z\to\hat{z}} \frac{S(z,\hat{z})}{z-\hat{z}} \tag{2.28}$$

$$= \lim_{z\to\hat{z}} \left\{ -b\,\hat{z}\,\frac{u(z,\hat{z})-u(\hat{z},\hat{z})}{z-\hat{z}} + b\sum_{n\geq 2}\frac{g(n,z,\hat{z})}{n} - C \right\} \tag{2.29}$$

$$= -\,b\,\hat{z}\left.\frac{du(z,\hat{z})}{dz}\right|_{z=\hat{z}} + b\sum_{n\geq 2}\frac{1}{n}\left.\frac{dg(n,z,\hat{z})}{dz}\right|_{z=\hat{z}} - C \tag{2.30}$$

(the sum being in practice bounded, as group size necessarily has an upper limit, the interversion of the limit and the sum is valid).

To carry on with the calculations, an approximation is needed. For very large groups, the second term tends to become very small compared to the two others. For instance, in the case of the aggregation toy model, calculations show that it converges to 0 as $T \to +\infty$. Below, I simply neglect it (but see the discussion afterwards). Denoting

$$h(\hat{z}) = - \left. \frac{du(z,\hat{z})}{dz} \right|_{z=\hat{z}} \tag{2.31}$$

we obtain

$$\left. \frac{dS(z,\hat{z})}{dz} \right|_{z=\hat{z}} \approx b\,\hat{z}\,h(\hat{z}) - C \tag{2.32}$$

or, in a more 'readable' form:

$$dS(z,\hat{z}) \approx b\,\hat{z}\,h(\hat{z})dz - Cdz \tag{2.33}$$

Noticing that $h(\hat{z})$ is the variation in the probability for an individual to join some group if she deviates with an infinitesimal positive quantity from the resident social trait, it can reasonably be assumed, in the general case, that $h(\hat{z}) > 0$: being more social decreases the risk to remain ungrouped. Then, the interpretation of the obtained formula is straightforward: the variation in growth rate induced by a small mutation in the social propensity is equal to the increased chance it gives to join a group, times the payoff drawn from the group (i.e., $b\,\hat{z}$), minus the marginal, additional cost paid:

$$\text{increase in growth rate} = \text{earned probability to be in a group} \times \text{group payoff} - \text{additional cost} \tag{2.34}$$

If $z > \hat{z}$, that is, for a pro-social mutation to invade, the grouping opportunities earned compared to the residents must be sufficient to offset the additional cost: this is a very general condition analogous to many established in the literature for other mechanisms. Lastly, let us remark that not neglecting the term $b\sum_{n\geq 2} 1/n \; dg(n,z,\hat{z})/dz|_{z=\hat{z}}$ (for instance, if groups are not large enough) makes the growth rate's derivative more positive; therefore, the invasion of a positive mutation easier: once again, social behaviors are easier to establish in small groups.

2.5.3 Application to an aggregation process

Coming back to the toy aggregation process of the two-strategy analysis, the relevant continuous trait here is $z = \pi$, i.e. the individual tendency or probability to stick to another individual ($z \in [0,1]$). We assume T to be very large, so that every recruiter is a resident: therefore the probability for an individual to join a group is $\hat{z}$ if she is a resident and $\sqrt{\hat{z}z}$ if she is a mutant (in the two-trait model, $\mathbf{A}-\mathbf{A}$ adhesion occurs with probability $\pi_{aa} = \sqrt{\pi_{aa}\pi_{aa}}$, $\mathbf{S}-\mathbf{S}$ with probability $\pi_{ss} = \sqrt{\pi_{ss}\pi_{ss}}$ and $\mathbf{A}-\mathbf{S}$ with probability $\pi_{as} = \sqrt{\pi_{aa}\pi_{ss}}$). Hence $u(z,\hat{z}) = 1-\sqrt{\hat{z}z}$ and $h(\hat{z}) = 1/2$. The condition for a small pro-social mutation to invade is then that

$$\hat{z} > \frac{2C}{b} \tag{2.35}$$

Further calculations not showed here (involving second derivatives) make it possible to characterize the singular point $z^* = 2C/b$ as a repellent equilibrium that is not convergence-stable, invasible and does not allow for protected polymorphism.

In the end, given those aggregation rules, a monomorphic population can be invasible by more and more social mutations until $z = 1$ (full sociality), provided the starting common trait is greater than z^*. Below this threshold, pro-social mutations cannot invade while anti-social can, until $z = 0$ (full asociality) in the whole population. Notice that, as previously, this holds in the case when T is infinitely large. When T is finite, the term we neglected may not be rightly so, so that pro-social mutations can invade for a wider range of initial social traits in the population; in other words, the condition $\hat{z}_0 > z^*$ is alleviated as groups get smaller.

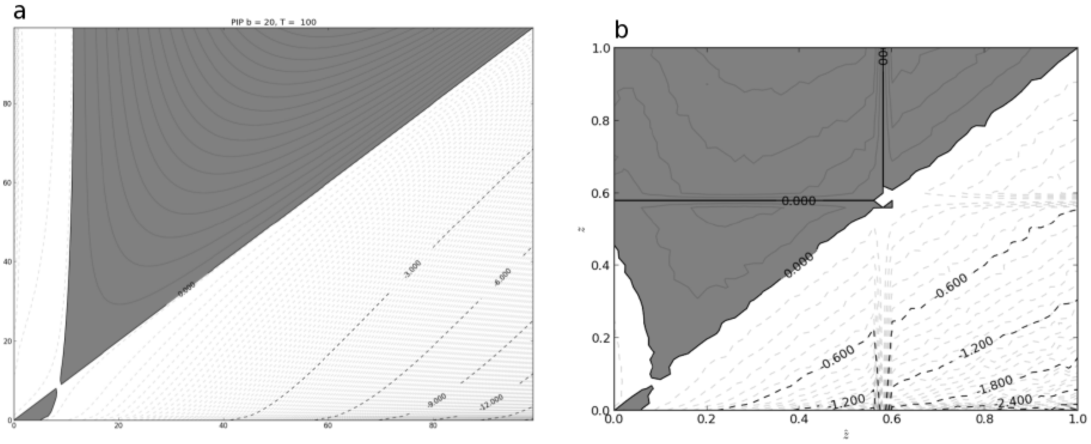

Figure 2.10: Analytical and computational pairwise invasibility plots for the continuous model

A positive invasion fitness (gray) means that the mutant can invade the population and replace the resident trait whereas a negative invasion fitness (white) means that the mutant is outcompeted. In the analytical PIP, the singular strategy z around $z = 0.1$ is an evolutionary stable strategy (ESS: it cannot be invaded by nearby mutants) but is not convergence-stable. The system is thus bistable: if the resident trait is smaller than z, more and more asocial mutants invade the population until it is fully asocial ($\hat{z} = 0$) and no group can form anymore; if the resident phenotype is greater than z^*, the population evolves toward $\hat{z} = 1$ and the disappearance of singletons. Both PIP have a similar structure around the first diagonal, which is the only portion relevant for gradual evolution. However, while the non-convergence stability of z^* is unchanged in the computational PIP, the ESS-stability is lost. Figure produced by G. Doulcier.

The pairwise invasibility plot (PIP) summarizes those results (Fig. 2.10). The effect of the benefit-to-cost ratio b/c and the patch size T on the PIP is displayed in Figure 2.11.

2.5.4 Condition for altruism

For a social mutation $z = \hat{z} + dz$, to be altruistic means that, in the resident population structure entailed by the $\hat{z}$ trait, an individual switching from the resident strategy $\hat{z}$ to the mutant strategy z would not get net positive benefits. The resident population structure is defined by $g(n, \hat{z}, \hat{z})$. A mutant in such population structure would get a net payoff of

$$b \sum_{n \geq 2} g(n, \hat{z}, \hat{z}) \, \frac{z + (n-1)\hat{z}}{n} - Cz \tag{2.36}$$

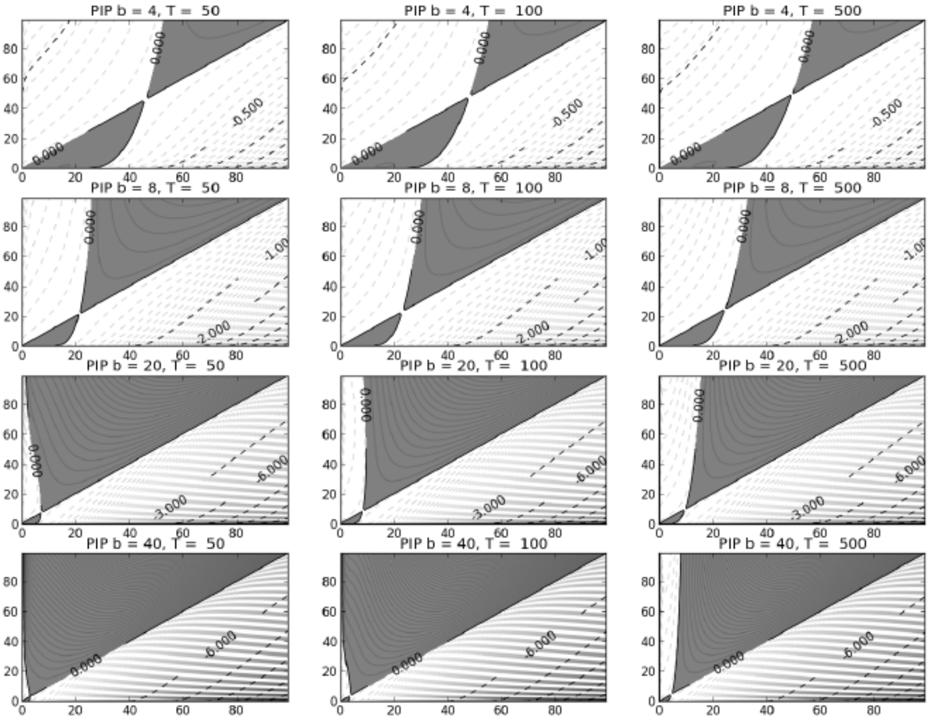

Figure 2.11: Sensitivity of the pairwise invasibility plot on parameters b/c and T

The invasion fitness is here computed applying the analytical method. The structure of the PIP and the nature of the equilibrium z^* is largely independent of the parameters, but its position changes: when b/c increases, sociality is more easily promoted and z^* decreases. Smaller values of T also tend to decrease z^* (albeit to a smaller amount); this is consistent with the well-known facilitating effect of small group sizes on social behavior. Figure produced by G. Doulcier.

while a resident gets

$$b \sum_{n \geq 2} g(n, \hat{z}, \hat{z})\, \hat{z} - C\hat{z} \tag{2.37}$$

Therefore, the social mutation is altruistic if

$$b \sum_{n \geq 2} g(n, \hat{z}, \hat{z})\, \frac{z + (n-1)\hat{z}}{n} - Cz < b \sum_{n \geq 2} g(n, \hat{z}, \hat{z})\, \hat{z} - C\hat{z} \tag{2.38}$$

i.e. whenever

$$
\begin{aligned}
& b \sum_{n \geq 2} g(n, \hat{z}, \hat{z}) \, \frac{z - \hat{z}}{n} < C(z - \hat{z}) \\
\iff \quad & \frac{b}{c} < \left[\frac{g(n, \hat{z}, \hat{z})}{n} \right]^{-1} := r_{alt}(\hat{z}) \qquad (2.39)
\end{aligned}
$$

This condition is comparable to that found in the discrete model (eq. 2.15). The threshold $r_{alt}(\hat{z})$ is homogeneous to a group size. Indeed, excluding loners, the mean group size in the population is:

$$
\hat{\gamma}_{\hat{z}} = \frac{\sum_{n \geq 2}^{T} n \Gamma(n)}{\sum_{n \geq 2}^{T} \Gamma(n)} \qquad (2.40)
$$

where $\Gamma(n) = \dfrac{1}{T} \dfrac{g(n, \hat{z}, \hat{z})}{n}$ is the number of n-sized groups. Thus,

$$
\begin{aligned}
\hat{\gamma}_{\hat{z}} &= \frac{\sum_{n \geq 2}^{T} n \frac{1}{T} \frac{g(n,\hat{z},\hat{z})}{n}}{\sum_{n \geq 2}^{T} \frac{1}{T} \frac{g(n,\hat{z},\hat{z})}{n}} = \frac{\sum_{n \geq 2}^{T} g(n, \hat{z}, \hat{z})}{\sum_{n \geq 2}^{T} \frac{g(n,\hat{z},\hat{z})}{n}} \\
&= (1 - u(\hat{z}, \hat{z})) \, r_{alt}(\hat{z}) \qquad (2.41)
\end{aligned}
$$

As the proportion of ungrouped individuals $u(\hat{z}, \hat{z}) = 1 - \hat{z}$, we finally get:

$$
r_{alt}(\hat{z}) = \frac{\hat{\gamma}_{\hat{z}}}{\hat{z}} \qquad (2.42)
$$

2.6 Discussion

2.6.1 Social groups formation and evolution

In this work, I address the coupling between the process of group formation and the evolutionary dynamics of individual “social” traits that affect both aggregation propensity and group cohesion, e.g. cell-to-cell adhesiveness. In addition to entailing a different contribution to group welfare, such traits underpin a difference in expected group size distributions. This difference ultimately generates assortment at the population level even in the absence of preferentially directed interactions based on peer recognition. Rather, I evidence that, whenever the size of groups is not fixed, simple non-assortative rules can still generate average local environments that favor the evolution of sociality even when it is not associated to direct benefits. This claim is illustrated by a toy model where groups form by blind interactions among individuals with different attachment abilities, stemming for instance from signalling or due to the production of a costly glue. This deliberately simple setting shows that even when attachment rules are indiscriminate toward the strategies of partners (and groups of any size are randomly assorted), socials individuals fare better than asocials thanks to the distinct allocations of the two types in group of various sizes and in particular to different chances of ending up alone. The emergent population structure gives rise to a Simpson's paradox where one strategy's advantage is reversed when one goes from the group to the population level (Box 2.4.). This has already been related to the evolution of cooperation when group size changes in time (Hauert et al., 2006a; Chuang et al., 2009). It is noteworthy that in the toy model there is no intrinsic limitation to the size of the evolutionarily viable groups, contrary to most previous models of N-player games, e.g. (Matessi and Jayakar, 1976; Powers et al., 2011). This suggests that sociality in large groups, such as in microbial communities, can be sustained with unsophisticated mechanisms that do not require information transfer between partners.

Box 2.4. The Simpson's paradox

The so-called Simpson's paradox (Chuang et al., 2009) encapsulates the counterintuitive situations that may arise when two levels of description conflict. Consider individuals, either cooperators or defectors, playing in groups and multiplying at rates that depend on their net payoffs. Within one group, every member gets the same benefit but cooperators pay an additional cost, so that defectors are always better off than their cooperating group partners. Yet, at the same time, groups where cooperators are overrepresented fare better than groups composed of many defectors to such extent that, in the gene pool of the global population, cooperation might rise in frequency. The Simpson's paradox is a purely statistical mechanism, but one that has a key role in evolutionary biology and is very much in line with arguments of group (or multilevel-) selection.

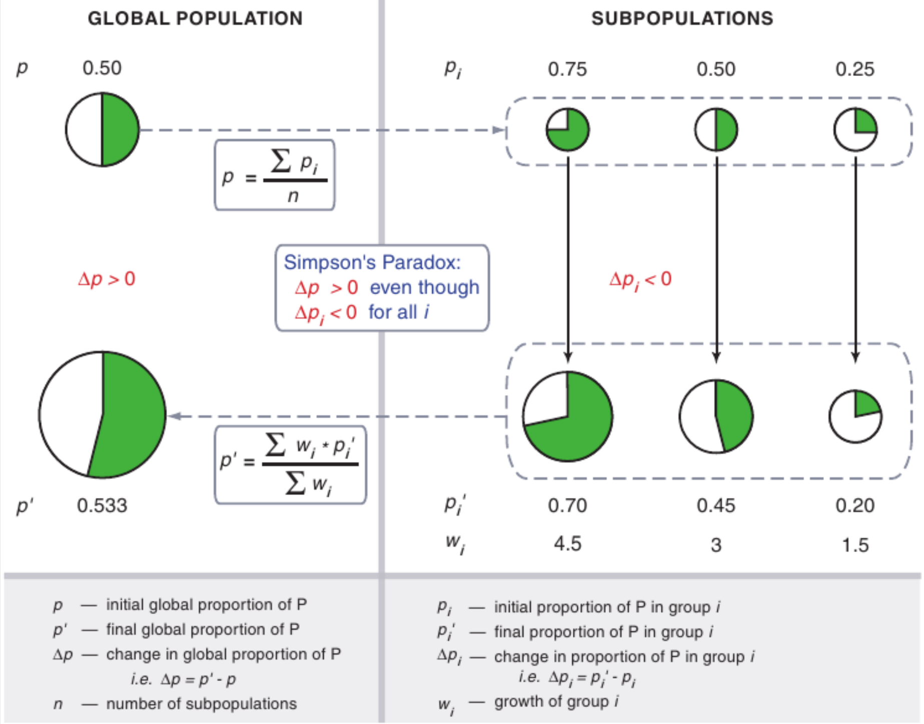

Figure 2.12: The Simpson's paradox

Simpson's paradox refers to a situation in which several groups, composed of two types of elements, P and NP, evolve so that the proportion of P elements decreases within each group but nevertheless increases in average overall. The right side shows the evolution of Simpson's paradox: three hypothetical subpopulations represented by pie charts of P (green) and NP (white) slices; the initial and final subpopulations are connected by solid black arrows. The left side shows the corresponding composition of the initial and final global population formed by these three subpopulations (dotted lines). As a whole, the figure illustrates the paradox of P decreasing in each subpopulation ($\Delta p_i < 0$ for every group i) but increasing overall ($\Delta p > 0$). This "paradox" is a purely statistical effect, based on the fact that the global proportion of P is a group size-weighted average that differs from the nonweighted average. In general, if we start from n groups of equal sizes and proportions p_i of P ($i = 1, \ldots, n$), whether Simpson's paradox is observed depends on the changes in proportion of P within each group, Δp_i, and on the overall growth of each group, w_i. Figure and caption taken from (Chuang et al., 2009).

2.6.2 Aggregative sociality in microorganisms

In the microbial world, the formation of biofilms and their cohesion are reckoned to be beneficial to cells in many respects (Velicer, 2003). In several microorganisms, the same costly individual traits that support the stability of groups may enhance the probabilities for cells to be part of them in the first place. Velicer and Yu featured costly "stickiness" as an adaptive prerequisite in swarming microorganisms (Velicer and Yu, 2003). In *D. discoideum*, the production of cell-adhesion molecules required for the aggregation cycle is thought to reduce the chances to become a spore: more adhesive strains are primarily found in the dead tissues of the fruiting body (Ponte et al., 1998; Strassmann and Queller, 2011). Myxobacteria form multicellular aggregates as well, that enhance survival by decreasing predation and favoring disperal (Shimkets, 1986a,b). Both agglutination and social cohesion are mediated in these bacteria by the production of a costly extracellular matrix of fibrils, increasing at the same same time cell adherence and enabling collective gliding (Velicer and Yu, 2003). Mutations that affect a gene located at a single locus impair fibril binding and result in both lower cell-cell adhesion and cohesion of aggregates (Shimkets, 1986b). In *S. cerevisiae*, an adhesion protein expressed by a social gene (FLO1) prompts individuals to form flocs that provide them with enhanced resistance to chemical stresses (Smukalla and al., 2008). When this strain is mixed with non-flocculating variants, heterogeneous aggregates still contain a majority of FLO1$^+$ cells, while individuals outside groups are more often FLO1$^-$, thus denoting assortment emerging from mere different adhesive abilities.

Although the processes involved in group formation become more complex as the cognitive abilities of players increase, our general conclusions might be also of interest for higher organisms that interact via mechanisms parallel to physical adhesiveness. For instance, Dunbar interpreted grooming in monkeys as a behavior likely to provide higher grouping opportunities as well as cement social bonding once the group is formed (Dunbar, 1993), and further extended the argument to humans, based on the presumed genetic foundations of language (Pinker and Bloom, 1990). Even if we have focused here on an aggregation mechanism that is more promptly related to social microrganisms, our conclusions hold in general for any inheritable trait, not necessarily involving physical adhesion, that plays a role both in group formation and group cohesion.

2.6.3 Nonnepotistic greenbeards?

In this model, assortment is generated among carriers of the social gene alone, and not on the whole genome. Therefore, sociality here pertains to green beard mechanisms as termed by the recent classification of Gardner and West (West et al., 2007b; Gardner and West, 2010). In their review, the authors stressed that such genes need not code for conspicuous traits as was posited in the original formulations (Hamilton, 1964; Dawkins, 1976). We argue that assortment at a single locus does not require nepotistic behavior of the gene towards other carriers neither, at least not in the usual sense imposed by dyadic or fixed-N frameworks. Indeed, assortment may mechanistically occur even when social individuals interact with each type in the same proportions as asocial individuals, provided they do it more often. A blind increase in the propensity to interact can thus have the same effect as preferentially directed interactions with peer discrimination, that may be more demanding on the cognitive level. This might be of interest for the interpretation of social behavior in organisms where the existence of recognition mechanisms is not straightforward. More in general, it might be useful to disentangle more explicitly green beard mechanisms that rely on active sorting of interaction partners from passive, indiscriminate mechanisms generating assortment with weaker requirements (Eshel and Cavalli-Sforza, 1982). Such differentiation would echo and complement that of obligate vs. facultative green beards formulated in the case of dyadic interactions (Gardner and West, 2010).

2.6.4 About altruism and direct benefits

An important point is that a cooperative trait is not altruistic or directly beneficial *per se*, but relative to a given population structure, that it itself contributes to shape. In particular, its status can change along an evolutionary trajectory. Let us plot the minimal benefit-to-cost ratio r_{min} necessary to promote sociality and the maximal benefit-to-cost ratio r_{alt} below which the social trait is altruistic in the toy model. According to eqs. (2.6) and (2.15),

$$r_{min}(x) = \left[\sum_{n=2}^{+\infty} \frac{1}{n} \left((n-1)\frac{(d_s(n) - d_a(n))x}{(d_s(n) - d_a(n))x + d_a(n)} + 1 \right) d_s(n) \right]^{-1} \tag{2.43}$$

and

$$r_{alt}(x) = \frac{1}{\displaystyle\sum_{n\geq 2} \frac{d_s(n)}{n}} \tag{2.44}$$

These two ratios are equal for $x = 0$. For $x = 1$ and large T, we can show that $r_{alt} \simeq T$. Figure 2.13 displays $r_{min}(x)$ and $r_{alt}(x)$ as a function of x for a given set of parameters. We can distinguish four cases:

1. when $b/c \geq r_{alt}(x = 1)$, sociality can evolve from scratch as it is always directly beneficial. If maximal group size is large, this corresponds to the usual condition $b/c > T$ for sociality to evolve via direct benefits in groups of size T.
2. when $r_{min}(x = 0) \leq b/c < r_{alt}(x = 1)$, sociality can evolve from scratch and switches from directly beneficial to altruistic as x increases. This is due to the fact that when the population is poorly social, groups are smaller and the marginal gain retrieved by one's own social contribution cancels its cost.
3. when $r_{min}(x = 1) \leq b/c < r_{min}(x = 0)$, sociality steadily evolves as soon as it reaches some threshold frequency x^* such as $b/c = r_{min}(x = x^*)$. All along the evolutionary dynamics, the social trait is altruistic.

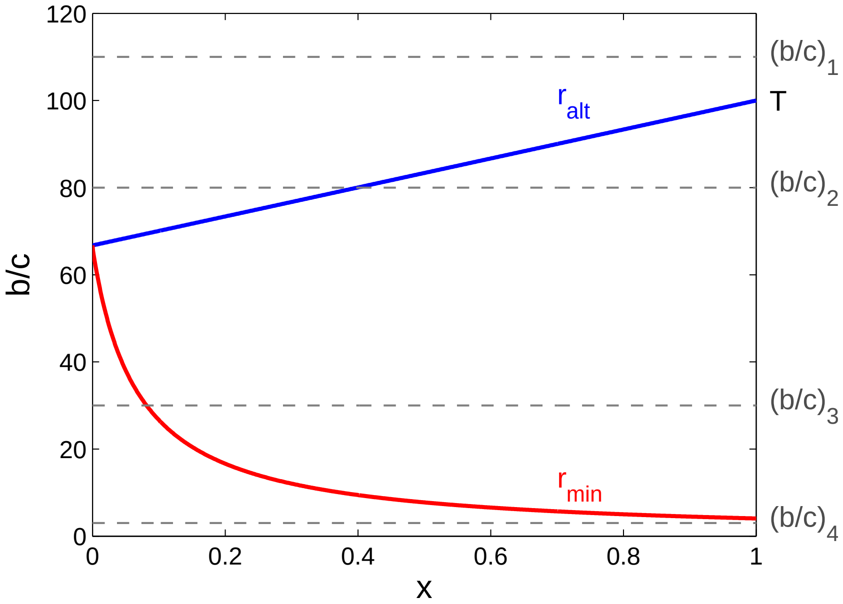

Figure 2.13: Minimal b/c ratio to promote sociality vs. maximal b/c ratio for sociality to be altruistic.

According to the benefit-to-cost ratio, we distinguish four cases: 1) directly beneficial sociality evolves from scratch (e.g. $(b/c)_1$); 2) sociality evolves from scratch by direct benefits but becomes altruistic during the evolutionary trajectory (e.g. $(b/c)_2$); 3) altruistic sociality can evolve only from a threshold frequency x^* (e.g. $(b/c)_3$); 4) sociality never evolves (e.g. $(b/c)_4$). The benefit-to-cost ratio thus also influences the "status" of the social trait, and this status can change along the evolutionary trajectory.

4. when $b/c < r_{min}(x = 1)$, (altruistic) sociality can never prosper and the population is doomed to full asociality.

This suggests that in real microbial populations, a social trait is likely to change status along its rise in frequency in the population: the advent of sociality might be first triggered by a relaxed social dilemma because the groups that form are still small. When the social frequency rises, positive assortment between socials makes it possible for sociality to attain fixation even though it has become an altruistic trait.

2.6.5 Toward a re-evaluation of the group formation step

I have stressed that the process of group formation can play an essential role in the unfolding of the evolutionary dynamics of social traits. A complete account of the evoution of cooperative groups requires to trace back the entire process leading to their formation. The toy model used here is a useful tool to illustrate my conclusion in a simple and extreme setting. It is however missing many features of actual biological systems. One could instead wish to predict, based on individual properties of physical attachment, the group size dynamics and the degree and nature of assortment between the social and asocial types in a more realistic aggregation model. This requires to further specify the mechanism of group formation, and notably explicit the individual rules of interaction and the topology structuring individual encounters. For organisms moving on a plane, such as cells gliding on a surface, grouping patterns and the resulting group size distributions have been mimicked by models based on simple rules (e.g. Okubo, 1986; Vicsek et al., 1995; Bonabeau et al., 1999). Recently, social games have been implemented in explicit schemes of aggregation for self-propelled particles interacting locally with their neighbors (Chen et al., 2011a,b). The way aggregative traits themselves can be sustained in a landscape shaped by a realistic group formation process however is still to be explored. Yet, the propensity to seek interactions, before that of behaving altruistically once the interaction is established, may be the very first, and a prerequisite, of all social actions.

Chapter 3

Differential adhesion between moving particles for the evolution of social groups

This chapter (minus section 3.5) is adapted from "Garcia, T., Brunnet, L.G., and De Monte, S. Differential adhesion between moving particles as a mechanism for the evolution of social groups", in review in Plos Computational Biology.

3.1 Introduction

3.1.1 Main issue

The ability to form and sustain collective ventures is observed at all levels of the living world, spanning from human societies to microbial populations. In many biological settings, grouping requires individual traits that are costly for their carriers (Velicer, 2003; Xavier, 2011; Schtickzelle et al., 2009). Sociality is thus an apparent paradox of evolutionary theory, as asocial "cheaters" who do not contribute to social welfare but reap group benefits should be favored by natural selection. This issue, that was first raised by Charles Darwin, has been revived in the last decades and is still pivotal in evolutionary biology, giving rise to an extensive literature on the evolution of cooperation.

The difficulty to explain the evolutionary emergence and maintenance of cooperation is particularly acute when the organisms diplaying social behavior are relatively simple such as microbes, so that they cannot rely on the complex cognitive and cultural abilities that are usually invoked as supporting cooperation in animals. Such simpler interactions and behaviors, together with the ease of cultivating bacterial populations in controlled environments, offer on the other hand the opportunity to address elementary mechanisms that underlie the evolution of sociality in general settings (Velicer, 2003; Crespi, 2001; West et al., 2007a; Celiker and Gore, 2013).

Here, I consider the evolution of a social (adhesive and cooperative) trait in a population with a life cycle of aggregation-reproduction-dispersal, commonly observed in microbes displaying high degrees of cooperation, such as social amoebae or Myxobacteria (West et al., 2007a). In such cases, the existence of recurrent chimeric aggregates of potentially unrelated individuals appear to contrast with the classic expectation that cooperative behavior should be expressed to a lesser extent the weaker the genetical relatedness within social groups. I make the aggregation phase explicit by modeling cells as self-propelled particles moving on a plane, and study under which conditions social traits evolve through natural selection, and to what spatial patterns they are associated.

Game theory has been long used to account for the evolutionary sustainability of genetically determined cooperative traits that benefit others while being costly to the individual (Hofbauer and Sigmund, 1998). Several different formalizations have been proposed to describe the effect of an individual's trait and its interactions on its own reproductive success. Among those, cooperation in social settings is classically modeled as N-player games, where fitness depends on the features of the group. The simplest formulation of such games is the Public Goods Game (PGG) (Olson, 1971), where the benefits yielded by the group depend on the fraction of cooperators in it.

In questioning the mechanisms by which cooperative behavior can prosper, most models consider environments where group size is constant and independent of individual strategies. A growing number of studies has recently started to address cases when the interaction topology, and notably the size of the social groups, is an emergent property of individual-level features. These studies have modeled specific rules for entering groups with limited carrying capacity (Avilés, 2002; van Veelen et al., 2010); evolvable preferences for group size (Powers et al., 2011); competition for the use of a diffusible compound (Nadell et al., 2010), or for empty space (Pfeiffer and Bonhoeffer, 2003; Hauert et al., 2006a); the voluntary participation to groups (Hauert et al., 2002a,b); but also differential attachment supported by the cooperative trait (Pacheco et al., 2006; Garcia and De Monte, 2013). In many cases however, group formation has been modeled in well-mixed populations, or on a regular lattice where each individual occupies a cell and has a constant number of partners. While these assumptions are justified whenever individuals are either extremely motile or sessile respectively, they fall short in describing self-structuring traits in microbial populations with complex grouping patterns. More realistic models for the formation of groups from initially sparse individuals thus require an explicit account of particle movement in space and of the interaction forces that underpin the emergent "social landscape".

With this respect, Self-Propelled Particles (SPP) models have proved useful to account for the formation of collective structures (e.g. swarms) based on simple local rules for interaction. Although SPP models have now become a primary tool to address collective behavior both in the physical and biological sciences, the exploration of their interplay with the evolutionary dynamics of individual traits is still in its infancy (but see Guttal and Couzin (2010); Chen et al. (2011a,b); Zhang et al. (2011a); Perc et al. (2013)).

3.1.2 Outline

In this chapter, I explore the conditions for a genetic costly trait that enhances interactions to evolve in a population, in a context where the aggregation scheme is explicit and the ecological and evolutionary timescales are separated. In the Model section, I define a SPP model in which particles exert interaction forces on their neighbors whose intensities differ according to their strategies, social (**S**) or asocial (**A**). After a fixed number of time steps, individuals are assigned a fitness according to their strategy and the cohesiveness of their group. In the Results section, I discuss the ecological dynamics of aggregation and the evolutionary trajectories of the social frequency across generations, I highlight the key role of microscopic parameters on the evolutionary dynamics, and stress that sociality might be promoted only in specific ecological contexts. Finally, after discussing the main results, I extend the analysis to include cases in which individuals are able to reproduce during the aggregation phase, i.e. cases when ecological and evolutionary time scales are no longer separated.

3.2 Model

In this section, I motivate and describe a model which combines a Self Propelled Particles framework and a linear Public Goods Game. Cells are modeled as a population of particles differing in their adhesineveness that undergo successive cycles of aggregation, reproduction and dispersion, so that groups are "ephemeral", and not persistent, structures (Godfrey-Smith and Kerr, 2009). Such description is not only relevant to understand the evolution of facultative multicellular microbes, it also provides a "thought experiment" to test hypotheses on the origins of multicellularity itself (Michod and Roze, 2001; Godfrey-Smith, 2008; Sachs, 2008). In the case when groups are persistent, the evolution of cooperation is made easier by mechanisms such as colony growth, low dispersal and incomplete separation after cell division (Nadell et al., 2010; Kümmerli et al., 2009; Koschwanez et al., 2011; Van Dyken et al., 2013).

Within a cycle, the aggregation phase is ruled by a SPP (section 3.2.1) and is followed by a reproduction phase where particles leave offspring according to their payoff in a PGG (section 3.2.2). Particles are then dispersed, so that interactions in the following generation bear no memory of their previous positions. At the following generation, groups are thus formed again by genetically unrelated individuals. Iterating this cycle across many generations, it is possible to compute the evolutionary trajectory of the social trait (section 3.2.3).

3.2.1 Aggregation model

Here, I sketch a minimal model for collective motion that represents microbial populations with self-propelled particles moving on a plane. This kind of models has been widely explored in statistical physics (e.g. Vicsek et al. (1995); Grégoire et al. (2003); Grégoire et Chaté (2004)), demonstrating that simple short-range interactions are sufficient to achieve spatial repartition of particles (typically of one single type) into clusters.

More in particular, it draws inspiration from Myxobacteria and Dictyostelids, that upon nutrient exhaustion abandon a solitary lifestyle to form multicellular aggregates. Even though interactions between cells in these aggregation processes are very complex, and several models have directly addressed specific features (e.g. the role of cyclic AMP oscillations and chemotaxis in the aggregation of *D. discoideum* (Guven et al, 2013), or that of the rod shape in *M. xanthus* streaming (Peruani et al., 2012)), the present model retains only few essential characteristics of the aggregation process and investigates their evolutionary consequences.

In the absence of interaction, cells display a persistent random walk – i.e. with correlation between successive step directions (Codling et al., 2008) – as observed in the vegetative phase of Dictyostelium life cycle (Li et al., 2011; Golé et al., 2011), the directed and stochastic components being modeled here by force and noise terms. The interaction forces may in practice result from chemotaxis or adhesion proteins at the cell surface (Coates and Harwood, 2001).

Natural microbial populations display differences in interaction modes (for instance, in stickiness or responsiveness to chemotaxis) that are often associated with differences in the capacity of specific strains to be overrepresented in spores (Strassmann and Queller, 2011). The modeled populations is composed of particles of two types –“social” (**S**) and “asocial” (**A**) – that have distinct interaction forces intensities, **S** particles being more attractive than **A** particles.

The interaction strategy is deemed genetically encoded and unconditional. Previous models in which self-propelled particles differ in some microscopic feature (e.g. adhesion or motility) have been designed to study cell sorting within tissues (Belmonte et al., 2008; Beatrici and Brunnet, 2011; Zhang et al., 2011b), where the phase of aggregation from a dispersed initial condition was irrelevant.

Consider a population of N_{pop} particles, either **S** or **A**, moving on a square of side L with periodic boundaries (so that it is actually a torus). Irrespective of the orientation of their velocity vector **v**, particles move all at the same speed $v = ||\mathbf{v}||$, reflecting the inherent ability of propulsion of cells. Every particle has a finite spatial extension and exerts an interaction force on other particles as a function of their distances. Let us consider a particle indexed j of type $\sigma(j) \in \{\mathbf{S}, \mathbf{A}\}$. A second particle $k \neq j$ exerts a force $\mathbf{f_{jk}} = f_{jk}\mathbf{u_{jk}}$ (where $\mathbf{u_{jk}}$ is a unitary vector directed from j to k) upon the focal particle j. The dependence of the force f_{jk} on the distance $r_{jk} = ||\mathbf{x_j} - \mathbf{x_k}||$ between particles j and k is illustrated in Figure 3.1. It is infinitely repulsive at short range (within a hard-core radius r_0 to account to the particle's spatial extension), null at long range (above the interaction radius r_1) and is otherwise a linear elastic force:

$$f_{jk} = \begin{cases} -\infty & \text{if } r_{jk} < r_0 \\ -f_0 + \dfrac{r_{jk} - r_0}{r_1 - r_0}(\beta_{\sigma(j)\sigma(k)} + 1)f_0 & \text{if } r_0 \leq r_{jk} \leq r_1 \\ 0 & \text{if } r_{jk} > r_1 \end{cases} \tag{3.1}$$

This force reflects the existence of a finite action range of a glue, that keeps cells apart at an equilibrium distance around which they fluctuate below a cut-off radius. Cells may also interact via signaling, so that the interaction potential is continuous. It is expected that as long as the interaction remains short-range, the model will be qualitatively unaffected, as occurs to the phase diagrams of SPP models where different kinds of forces have been tested (Grégoire et Chaté, 2004; Belmonte et al., 2008).

The coefficient $\beta_{\sigma(j)\sigma(k)}$ tunes the effect of the force exerted by k on the movement of j, which

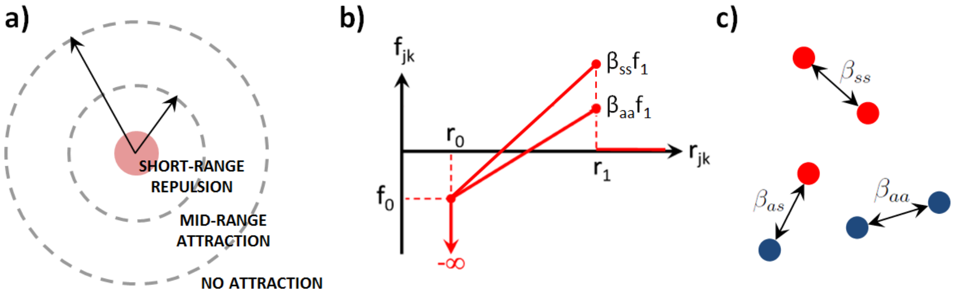

Figure 3.1: Local rules for interaction

Local rules for interaction: a) each individual undergoes an interaction force from its close neighbors (i.e. within a radius r_1); b) this force is repulsive within a radius r_0 and becomes attractive until a radius r_1; c) the interaction forces between two individuals are modulated by a coefficient depending on their respective strategies: β_{ss} if both are social, β_{aa} if both are asocial and β_{as} if one is social and the other asocial. We assume $\beta_{ss} > \beta_{as} > \beta_{aa}$.

depends on the particles' types. It thus can take four values $\beta_{SS}, \beta_{SA}, \beta_{AS}$ and β_{AA}. Consistently with the hypothesis of differential attachment, I assume that $\beta_{SS} > \beta_{AS} = \beta_{SA} > \beta_{AA} > 0$. As a consequence, the equilibrium radius r_{eq} such that $f_{jk} = 0$ is shorter in **S-S** interactions than in **A-A** interactions (see Fig. 3.1 b). In the following, $\beta_{SS}, \beta_{AS}, \beta_{AA}$ are in geometric progression (that is, $\beta_{AS} = \sqrt{\beta_{SS}\beta_{AA}}$) so that sociality entails a *differential* propensity to attach to other particles, but not a *preferential* bias toward other **S** particles, when compared with asociality (Taylor and Nowak, 2006; Garcia and De Monte, 2013). This means that a focal **S** particle gets attracted to **S**s and **A**s in the same proportions as a focal **A** particle does, as $\beta_{SS}/\beta_{AS} = \beta_{AS}/\beta_{AA}$; only to a larger amount. This warrants that no preferential assortment of strategies takes place just because of the choice of interaction intensities parameters.

For each particle, the direction of motion θ is updated according to the resulting force; at time $t + \Delta t$, the velocity of particle j is $\mathbf{v_j}^{(t+\Delta t)} = v e^{\mathrm{i}\theta_j^{(t+\Delta t)}}$ where

$$\theta_j^{(t+\Delta t)} = \arg\left\{ \mathbf{v_j}^{(t)} + \alpha \sum_{k \neq j} \mathbf{f_{jk}}^{(t)} \right\} + \eta\, d\theta \tag{3.2}$$

with α a coefficient with dimensions of a speed/force (in what follows, $\alpha = 1$) and $\eta\, d\theta$ an additive noise randomly drawn between $-\eta\,\pi$ and $\eta\,\pi$: $d\theta \sim \mathcal{U}([-\pi, \pi])$. The position of each particle at time $t + \Delta t$ is computed accordingly:

$$\mathbf{x_j}^{(t+1)} = \mathbf{x_j}^{(t)} + \mathbf{v_j}^{(t+1)} \Delta t \tag{3.3}$$

The ecological dynamics resulting from this scheme of aggregation is detailed in section 3.3.1.

3.2.2 Social dilemma

The aggregation process is stopped after a fixed number of time steps t_f, that defines the "ecological" time scale of the system. t_f reflects the finite time before novel reproduction/death events. After aggregation, the population is segmented into groups according to a criterion described in Box 3.1.

Box 3.1. Determination of groups

Criterion 1: In order to calculate statistics on aggregation as well as individual payoffs, a robust procedure to determine groups from particle positions and movements in the last time steps is needed. A first step is to decide, for each particle, whether it is stuck with a group or not. A simple recursive procedure will then be applied on the individuals found to be in a group to clusterize the population. The results presented in the main text correspond to the following implemented criterion, based on the assessment of the influence of the resulting force undergone by an individual j over the update of its movement. The idea is that an individual in a group is under the influence of more attraction forces than a free individual. We then assess to what extent such forces affect the speed vector of an individual and we do it for n_{step} timesteps in order to average out time fluctuations. A free individual is one that does not undergo sufficient attraction forces enough times during the last n_{step} timesteps:

$$j \text{ is free } \Leftrightarrow \sum_{t=t_f-n_{step}}^{t_f} \mathbb{1}_{\left\{||\sum_k \mathbf{f_{jk}}^{(t)}||/v>1\right\}} < \gamma\, n_{step} \tag{3.4}$$

where γ is some threshold coefficient between 0 and 1 (e.g. 0.5).

This criterion focuses on *a priori* causes of aggregation, and allows for a more or less stringent definition of "grouped", by tuning γ. The result of a segmentation of the population into groups according to this criterion is shown in Figure 3.2.

Criterion 2 To check robustness, I also tested a second criterion that focuses on the effect of aggregation behavior on individuals and their movement *a posteriori*. It is based on the comparison of the distance covered by the focal individual j with that expected from a random walker. Indeed, for low to moderate noise values a grouped individual's movement is characterized by a shorter correlation length than with Brownian movement. We thus sample the positions of the individual j at n_{step} distinct, non-successive timesteps before the ending of aggregation, i.e. at times $\tau_0 = t_f - (n_{step} - 1)l_{step}, \ \tau_1 = t_f - (n_{step} - 2)l_{step}, \ \ldots \tau_{n_{step}-1} = t_f$, where l_{step} is the duration between two sampling events. If the cumulated distance covered by individual j if greater than the average cumulated distance covered by a random walker ($= v \cdot n_{step}\sqrt{l_{step}}$), it is considered free, otherwise it is deemed grouped:

$$j \text{ is free } \Leftrightarrow \sum_{k=0}^{n_{step}-1} ||\mathbf{x_j}^{(\tau_{k+1})} - \mathbf{x_j}^{(\tau_k)}|| > v \cdot n_{step}\sqrt{l_{step}} \tag{3.5}$$

This second criterion leads to comparable separations between grouped and nongrouped individuals as criterion 1 in most cases; for very large noise values (such that the interaction forces and current speed vectors play little role in the update of movement compared to the random component), it however inaccurately regards a proportion of individuals as grouped whereas none is, as correlation lengths are now all comparable to that of a random walker.

Once is decided which individuals are free and which are in a group, actual groups are determined applying a simple recursive procedure on grouped individuals: any grouped individual within a radius r_1 near another grouped individual belongs to the same group. In the end, for each individual j it is possible to compute the size n_j of its group as well as, if $n_j > 1$, the number s_j of social individuals in it.

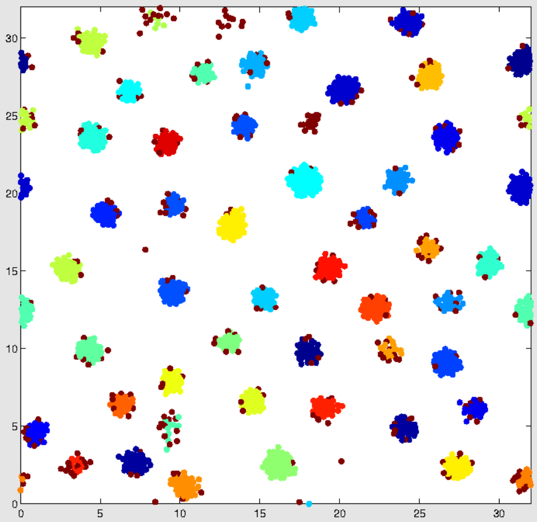

Figure 3.2: Segmentation of a structured population into groups

In this picture, each group is determined by criterion 1 and assigned a random color. Individuals that are deemed free are represented in dark brown. Some of them are isolated while others are found at the periphery of groups or within small, unstable groups.

Once aggregation is over, the reproductive success of every particle is determined as its payoff in a PGG played in its group. The common good at stake here is group cohesion itself, so that the payoff individuals derive from their group depends on the proportion of **S** members (Garcia and De Monte, 2013). Sociality thus plays a role both in the aggregation process and in the performance of groups. This assumption is consistent with what happens in several social microorganisms, where cell adhesion is a major factor determining the cohesiveness (and as a consequence, the viability) of cell aggregates (Ponte et al., 1998; Smukalla et al., 2008; Velicer and Yu, 2003). Equivalent assumptions have also been made in the theoretical literature, e.g. in (Simon et al., 2012): there, adhesive social cells entail higher group sizes and large groups are supposed to be more viable than small ones, leading to the maintenance of sticky cells through the interplay of individual and the group levels.

In a linear PGG, each **S** contributes b to group cohesion at a cost $-c$ to its reproductive success, whereas **A**s neither contribute nor pay a cost. Within a group, contributions are summed and shared among all members, irrespective of their strategy. Once again, an individual payoff can be split in a payoff due to self ($b/n - c$ for **S**s, as they get a share b/n of their own contribution and pay a cost $-c$, and 0 for **A**s) and a payoff due to the group co-members ($b/n\ \times$ the number of **S** co-players). Singletons do not earn any group benefits, and thus have a payoff of $-c$ or 0 according to their type. If an individual of strategy **S** or **A** belongs to a group of size n, $e_S(n)$ and $e_A(n)$ respectively denote the average number of **S** co-players in their groups. The average payoffs of an **S** and an **A** particle in groups of size n are thus:

$$P_S(n) = b\frac{e_S(n)}{n} + \frac{b}{n} - c$$
$$P_A(n) = b\frac{e_A(n)}{n}$$

If the social trait has no effect on the groups an individual belongs to (as for instance for randomly formed groups of fixed size N), there is no positive assortment between **S**s and $e_S = e_A$: sociality outcompetes asociality only when $b/N > c$, that is when a **S**'s share of its own contribution suffices to make its investment profitable (*direct benefits* case). Excluding this trivial case, sociality provides an advantage within groups of fixed size only if sufficient assortment within strategies ($e_S(n) > e_A(n)$) tips the balance in its favor (*altruism* case). In more general cases, when a group formation process produces groups of different sizes and different compositions, the social trait assumes a different status (directly beneficial or altruist) depending on the realized population structure, and may change along an evolutionary trajectory.

3.2.3 Evolutionary algorithm

The evolutionary trajectory of the population throughout successive generations is obtained by numerically evaluating the payoff of every particle at the end of the aggregation phase. At any given generation, the mean payoffs of **S**s and **A**s, which depend on the population structure at time t_f, provide their respective reproduction rates after a mere linear re-scaling between two boundary fitnesses (cf. Appendix D). Particles then may die, irrespective of their strategy, with a density-dependent mortality rate that keeps the total population size constant.

At the end of the generation, the resulting population is dispersed: the position and orientation of each particle is randomly assigned at the beginning of the next generation's aggregation phase. The complete re-shuffling of particles corresponds to the worst-case scenario in which assortment at one generation cannot be maintained (and enhanced) in evolutionary time. Sociality would be further favored if the spatial structure was inherited, so that cooperative traits may be boosted by groups engaging in between-group competition (Fletcher and Zwick, 2004; Cremer et al., 2012).

The probability to leave offspring is obtained normalizing the particle's payoff in a range $\{f_{min}, f_{max}\}$. For weak selection strengths (i.e. small $f_{max} - f_{min}$), the evolutionary trajectory generated by this algorithm is well approximated by a continuous-time replicator equation. According to this equation, the only determinant of the variation in **S** frequency is its average payoff advantage with respect to the **A** strategy. In section 3.3.2, I show that such average payoff can be expressed in terms that reflect different features of the population structure at the end of the aggregation phase.

In the simulations, the evolutionary algorithm is iterated for a number of generations (300) sufficient for the frequency in the population to reach a stable equilibrium state. The algorithm is described with more details in Appendix D. The nature of the evolutionary equilibria and their associated population structures are discussed in section 3.3.2. Section 3.3.3 describes how these evolutionary equilibria depend on the microscopic properties of the system: particle speed, noise intensity, interaction radius and density.

3.3 Results

Expliciting the process by which particles interact and form groups enables to study the interplay of the ecological time scale – relative to the aggregation phase – and the evolutionary time scale, over which the frequencies of social and asocial strategies change in the population. In the following sections, I will examine these time scales separately and eventually discuss what are the features at the particle level that support the evolution of sociality, and to what population structures this evolution is associated. Section 3.3.1 focuses on the outcome of the aggregation step within one generation. Section 3.3.2 addresses the evolutionary dynamics of the social trait across generations and highlights the role of *assortment* and *volatility* in determining the success of the social strategy. Finally, section 3.3.3 describes the dependence of the evolutionary equilibrium on microscopic parameters of motion and interaction.

3.3.1 Local differences in adhesion rule group formation and spatial assortment in the aggregation phase

Within one generation, particles interact for a finite number of time steps t_f, according to the numerical model described in section 3.2.1. Initialized in random positions, particles will aggregate or not in groups depending on the ecological parameters, analogously with what is observed for other models of SPP (Vicsek et al., 1995; Grégoire et al., 2003; Grégoire et Chaté, 2004). The simulations being halted before the asymptotic state is reached, I focus on the clustering of the population into groups that occurs on a fast time scale, and neglect all features such as group diffusion, merging and internal reassortment that occur on longer time scales. Slow relaxation to the asymptotic state mainly induces sorting within groups, which in this model has no fitness effect, hence no qualitative effect on the evolutionary outcomes.

The population forms groups in a broad range of the parameter space, but the size distribution of the groups and the proportions of grouped vs. free particles depend on the ecological parameters ruling particle motion and interaction. Movies of the aggregation process bear a strong resemblance with low magnification movies of the aggregation of *D. discoideum*, where initially dispersed cells form clumps of different sizes, while some cells keep moving outside the aggregates (Dubravcic et al., submitted).

The population remains scattered and no group is recognizable when directed motion overcomes the interaction forces. This occurs when the interaction cut-off radius r_1 is short; the population density $\rho = N_{pop}/L^2$ is small; the noise level η is high; the velocity v is large. Otherwise, local fluctuations are amplified and particles start to cluster until a quasi-steady state is reached where most particles are clumped into groups of different sizes, while some particles move in the "gas" phase between groups (Fig. 3.3). Within groups, each particle vibrates around an equilibrium position corresponding to the balance between all attractive and repulsive forces exerted by its neighbors, plus the noise component. Groups typically have a circular shape and are separated by a distance of the same order of magnitude as r_1.

In many parameters regions, and as long as β_{ss} and β_{aa} are different enough, groups display spatial segregation with more adhesive particles occupying equilibrium locations at the group core and less adhesive particles gravitating at the periphery in a unstable fashion. Such sorting within aggregates of cells with heterogenous adhesion, motility or chemotactic properties is a well-studied phenomenon (Graner and Glazier, 1992; Glazier and Graner, 1993; Belmonte et al., 2008; Beatrici and Brunnet, 2011; Zhang et al., 2011b; Bai et al., 2013). It resembles moreover the observed spatial segregation between WT flocculating cells and nonflocculating cells in species like *S. cerevisiae* (Smukalla et al., 2008). In more *ad hoc* models, the influence of within-group structure on particle fitness might be implemented. For instance, we expect the evolution of sociality to be further favored if the public good is explicitly modeled as a diffusible

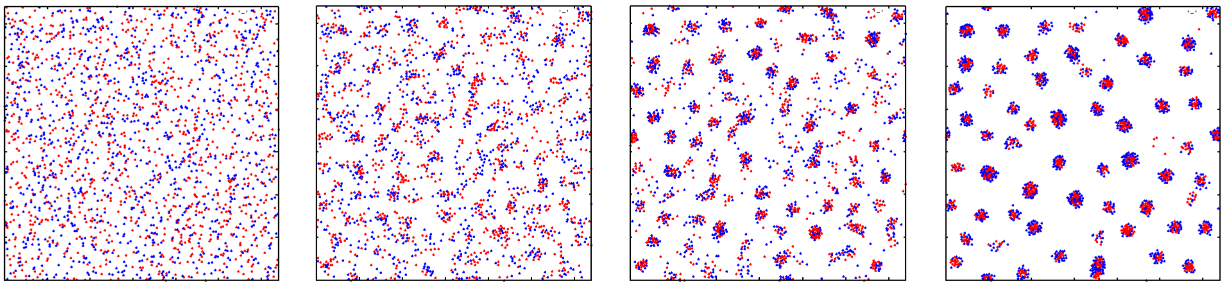

Figure 3.3: Snapshots of an aggregation process

Simulation of a population undergoing an aggregation process such as described in section 3.2.1, sampled at different timesteps. **S** individuals (red) are more adhesive than **A** individuals (blue). At each timestep, every individual updates its position and direction according to its neighbors within a radius r_1. Individuals begin to form clusters and then to spatially re-arrange themselves within clusters. Some of them may remain alone (not attached to any group). At the end of the aggregation phase, a spatial criterion makes it possible to distinguish groups and to find out each group's size and composition. Parameters: $N_{pop} = 2048, L = 32.0, x_0 = 0.05, v = 0.05, r_1 = 1.0, r_0 = 0.2, f_1 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 1.8, \beta_{aa} = 1.2, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, \eta = 0.3$.

substance (Driscoll and Pepper, 2010; Borenstein et al., 2013), thus reducing further the potential benefits of cheater cells that are found at the periphery of groups. (Julou et al., 2013).

3.3.2 Assortment and differential volatility between strategies drive the evolution of sociality

On the evolutionary time scale, the fate of the social type hinges upon the emergent structure of the population after the aggregation process. In simulations of the evolutionary dynamics, the population always stabilizes to a monomorphic equilibrium, either fully social or fully asocial. This is probably the consequence of the simple linear form of the PGG, which generally does not support the coexistence of different strategies, whereas payoff functions that are nonlinear in the fraction of **S** particles in a group have been shown to produce polymorphic equilibria (Archetti and Scheuring, 2010). The population structure that is achieved at the evolutionary equilibrium depends on the microscopic features of the dominant particle type, and falls under three categories: asocial and grouped; asocial and dispersed; social and grouped. A fully social dispersed equilibrium is always evolutionarily unstable: indeed, if **S** particles are unable to form clusters, they do not get any group benefits and are thus defeated by **A** particles that do not pay the cost of sociality. In the case of a fully asocial equilibrium, the population can either remain dispersed or grouped, depending on the ecological parameters.

Figure 3.4 recapitulates the evolutionary dynamics observed in the cases when sociality takes over the population. It displays the frequency x of **S** particles in the population through generations (Fig. 3.4a), starting from the initial condition $x_0 = 0.05$, and the spatial pattern achieved at the end of the aggregation phase (the ecological timescale is hidden here). **S**s initially have a higher average payoff than **A**s and thus replicate faster. The evolutionary feedback on the ecological time scale thus boosts **S** particles, that in turn give rise to larger groups, and ultimately leads to the fixation of sociality in the population. When **S**s are rare (Fig. 3.4b), group cohesion is low and most of the particles remain ungrouped. When x increases (Fig. 3.4c), groups are nucleated by a hard core of **S** particles. **A**s thus get less benefits from groups. Finally, when sociality has invaded the population (Fig. 3.4d), groups are much more cohesive and very few individuals are ungrouped. Mean group size saturates, and groups become denser since equilibrium distances are shorter among socials.

The condition for **S**s to be favored over **A**s depends on the game parameters b and c, as well as on the emergent population structure shaped by the ecological parameters (form and intensity of the forces, population size and density, noise level, velocity, radii of interactions) that govern the relative importance of diffusion (the persistent random motion) vs. cohesion (the interaction forces). If nonlinear payoff functions are chosen, the evolutionary success of sociality may as well depend on other game parameters, e.g. a threshold to activate the public goods (Archetti and Scheuring, 2010) or a synergy/discounting rate (Hauert et al., 2006b). Once the population structure is known, however, such condition can be expressed in terms of the evolutionary parameters and of two aggregated observables that quantify statistically the effect of population structure on particle assortment.

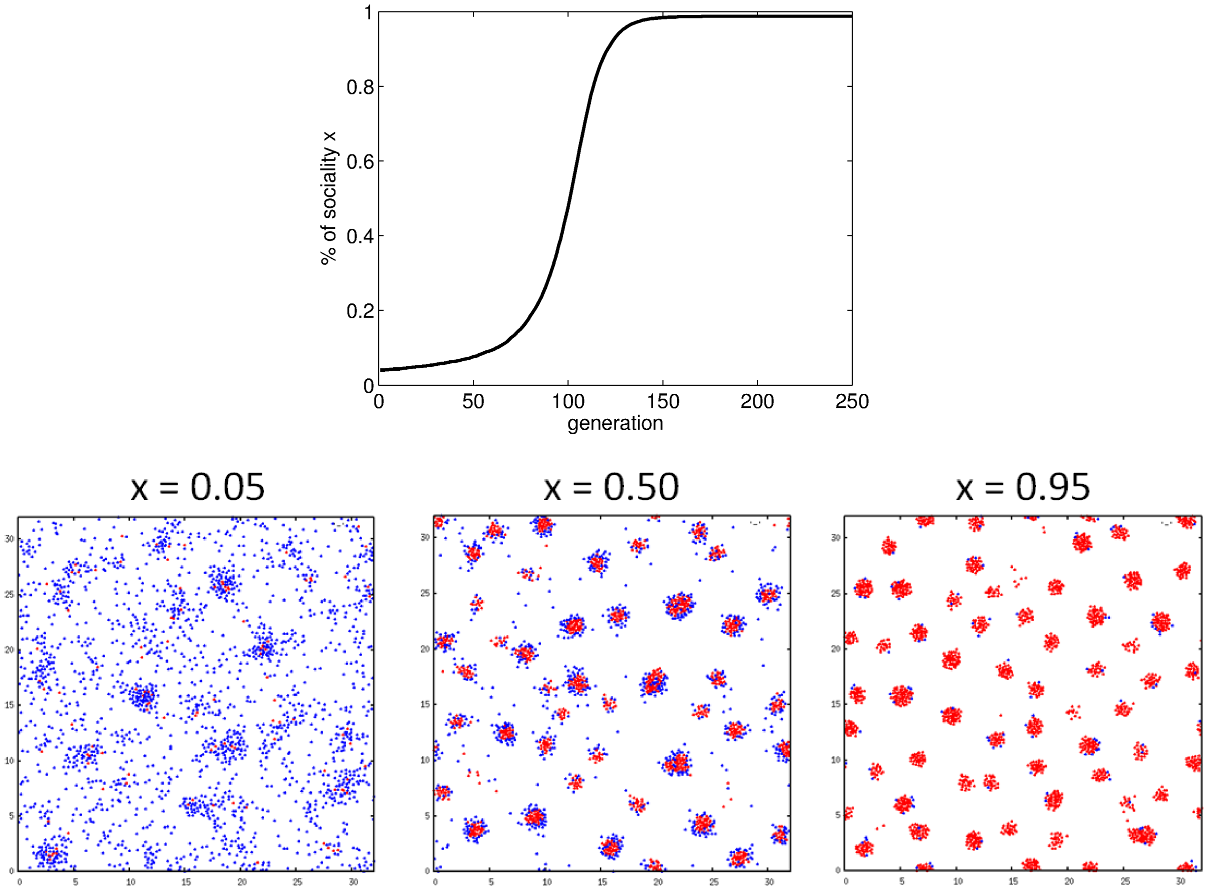

Figure 3.4: Evolutionary dynamics

Panel A: Evolutionary dynamics of the population: **S** mutants, initially in small frequency, are favored as they derive more net benefits from groups on average than **A** particles, and ultimately invade the population. Parameters: $N_{pop} = 2048, L = 32.0, x_0 = 0.05, v = 0.05, r_1 = 1.0, r_0 = 0.2, f_0 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 2.0, \beta_{aa} = 1.0, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, \eta = 0.3, b/c = 20$. Panels B, C, D: snapshots of the population after the aggregation step ($t = t_f$) at frequencies $x = 0.05$, $x = 0.50$ and $x = 0.95$ during the evolutionary trajectory depicted in panel A. As x increases, the population gets more and more clustered and free individuals fewer and fewer. When **S**s and **A**s coexist in the population, groups tend to be spatially segregated with **S** particles strongly bound at their core and **A** particles loosely attached at their periphery. As a consequence, more **S** particles find themselves grouped and **S**s tend to be better off than **A**s.

Following Garcia and De Monte (2013), a simple condition for sociality to be favored in a population after aggregation can be derived. Let us define u_S (resp. u_A) the proportion of **S** (resp. **A**) particles that remain *ungrouped* at the end of the aggregation step, and R_S (resp. R_A) the average fraction of **S**s experienced in the group of a focal **S** (resp. **A**) particle. According to the notations of section 3.2.2,

$$R_S = \frac{1}{1-u_S} \sum_{n \geq 2} \frac{e_S(n) d_S(n)}{n}$$

and

$$R_A = \frac{1}{1-u_A} \sum_{n \geq 2} \frac{e_A(n) d_A(n)}{n}$$

where $d_S(n)$ and $d_A(n)$ are the probability distributions for a **S** (resp. **A**) particle to be in a group of size n. The terms $1/(1-u_S)$ and $1/(1-u_A)$ appear as the these values are calculated conditioned to the fact that the **S** or **A** particle is not a singleton. The condition for the social trait to be favored at this generation is:

$$b(1-u_S)R_S + b \sum_{n \geq 2} \frac{d_S(n)}{n} - c > b(1-u_A)R_A \tag{3.6}$$

The $b \sum d_S(n)/n$ term in the LHS corresponds to the average marginal gain an **S** particle gets from its own contribution in the PGG within its group. The frequency of sociality therefore increases at the next generation as soon as the aggregation process entails sufficient differences in *assortment* (i.e. $R_S - R_A$ is large enough) or *volatility* (i.e. $u_A - u_S$ is large enough) between **S**s and **A**s.

Such two macroscopic quantities can be in principle measured experimentally in microbial populations by mixing two strains stained with different fluorescent markers. The main obstacle to quantify them precisely is a technical one: such measure requires to resolve single cells and at the same time to span a sufficiently wide field so that many aggregates are visible.

3.3.3 Parameters of motion and interaction condition the evolution of sociality

Sociality can get established as an effect of the feedback between ecological processes – linked to the emergence of particle aggregates – and the evolutionary change in frequencies of each type: it is favored when the microscopic aggregation parameters create a sufficient degree of assortment within groups and enhance group volatility. We explore now when these conditions are met as a function of four fundamental parameters underpinning particle motion and interaction: noise intensity, particle velocity, population density and interaction radius. The effects of changes in particle diameter can be also understood based on this analysis, since its value is directly obtained by rescaling the other parameters. Although in some cases random mutations and finite-size fluctuations are sufficient to cause the evolutionary invasion of social particles, most often the initial fraction x_0 of **S**s must exceed a threshold in order for the positive eco-evolutionary feedback to get established. Therefore, we initialized the system with $x_0 = 0.1$. The diagrams in this section illustrate how qualitatively different regimes can be attained as the microscopic parameters are changed, and how two different kinds of transitions between them are understandable with regard to the emergent population structure. They also display how the macroscopic observables u_S, u_A, R_S and R_A at the onset of the evolutionary dynamics (with $x_0 = 1$) change as a function of each parameter.

Noise intensity: The noise parameter η quantifies the extent to which random perturbations override the interaction forces between particles. A value of 0 for η corresponds to the case when a particle's direction at each timestep is completely determined by its current direction and the total force exerted by its neighbors. Conversely, a value of 1 means that its direction is chosen uniformly randomly within the range $[-\pi, \pi]$, so that the particle undergoes uncorrelated Brownian motion. A sharp transition is observed between a regime of clustered, highly social populations when noise is low and a regime where the population remains dispersed and asocial when the noise exceeds a threshold value (Fig. 3.5). In the first phase, noise is low enough to keep **S** particles together once they have joined a group, as they are bound by strong interactions forces. On the same timescale, instead, **A** particles, that are linked by weaker interactions, aggregate less (thus collecting less often group benefits than **S**s), and experience less social group environments when they do. Above the noise threshold, particles of any type become detached from each other and the population is highly volatile, as reflected by the concomitant drop in group sizes.

A certain level of inertia is thus required for a social variant to be selected in a population. This suggests that turbulent environments might be less favorable to the establishment of social behavior also because they hinder the formation of groups, other than because they offer a smaller number of niches to drive the evolution of more adapted types (Rainey and Travisano, 1998).

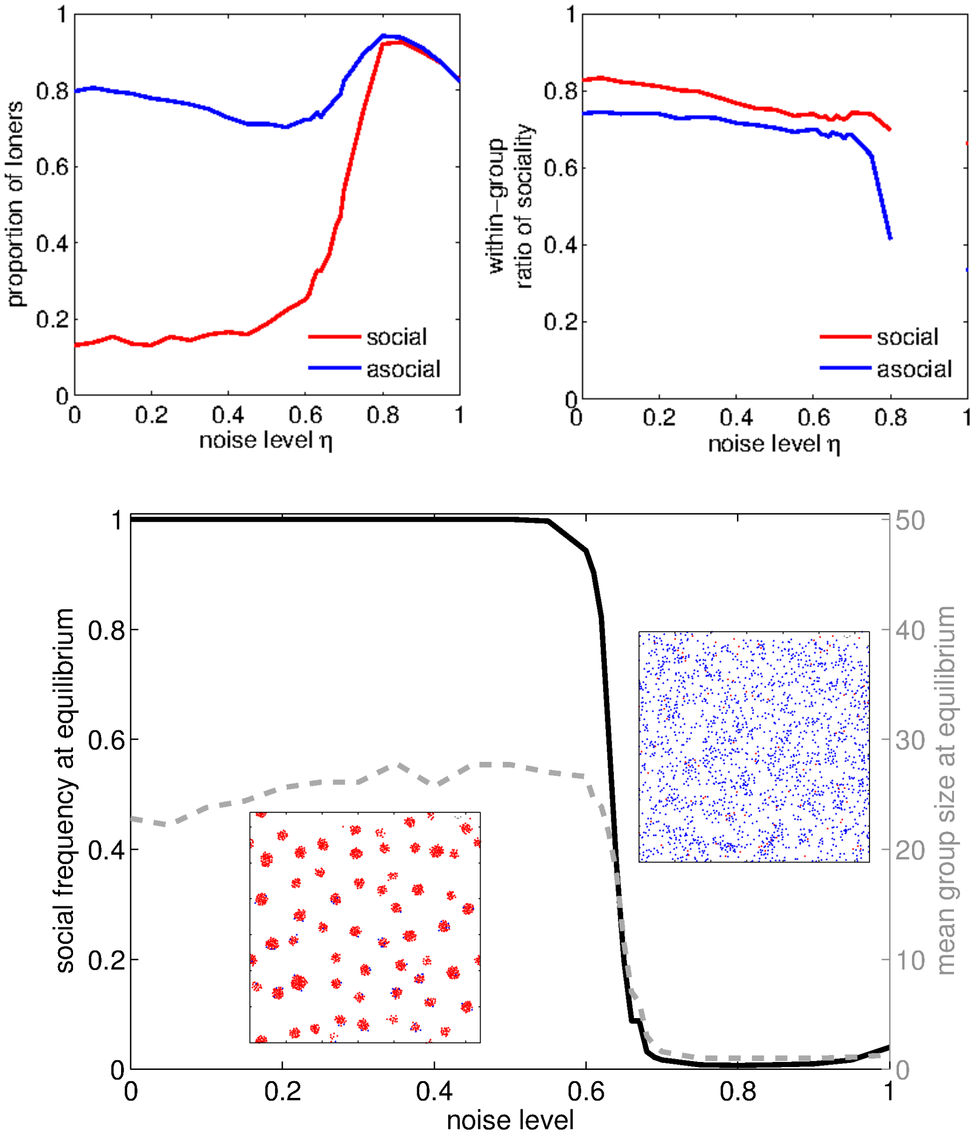

Figure 3.5: Effect of motion noise on u_S, u_A, R_S and R_A and on the evolutionary equilibria

Top: in general, **S** players are less often alone than **A** players ($u_S < u_A$): this differential volatility helps boost sociality. Moreover, positive assorment of **S**s occurs such that $R_S > R_A$. When noise is high however, both types are highly volatile so that **S**s cannot outcompete **A**s, and, as groups do not form anymore, social ratios R_S and R_A become irrelevant ; *Bottom*: Evolutionary endpoints and mean group size at equlibrium when the noise parameter η varies. Two phases can be observed: for low values of η, particles form groups and **S** players are favored until invasion of the population; for values of η exceeding a threshold, individuals are not able to aggregate anymore and sociality is no longer profitable: the final state is a dispersed, asocial population. Insets: representative snapshots of the population after the aggregation step ($t = t_f$) at the evolutionary equilibrium. Parameters: $N_{pop} = 2048, L = 32.0, x_0 = 0.05, v = 0.05, r_1 = 1.0, r_0 = 0.2, f_0 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 1.8, \beta_{aa} = 1.2, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, b/c = 20$

Particle velocity: The same effect observed for high values of noise also occurs for high velocities, that make interaction forces insufficient to hinder volatility. Figure 3.6 displays the same kind of transition from dispersed, asocial evolutionary equilibria to grouped, social populations as the velocity decreases. However, a transition of different nature can be seen when the velocity is diminished further. Groups keep forming when particles are slow, but their composition is mostly determined by the initial position of particles before aggregation, and is thus close to random assortment. Contrary to the transition occurring at higher velocity, groups keep existing across the transition, and their size does not drastically vary. The intermediate interval where sociality thrives corresponds to speeds that are sufficient to hinder cohesion among **A**, but not **S** particles.

The conflict between diffusion and cohesion (i.e., between speed of movement and interaction forces) thus results in a range of velocities where **S** particles are assorted and poorly volatile, while **A** particles are strongly volatile. Elsewhere, either **S**s are too poorly assorted, or the population too volatile. This suggests that the environments that promote social adhesion are those that are neither too fluid nor too viscous. These results are consistent with other recent studies: Meloni et al. (2009) discuss a model in which agents move freely with constant speed on a 2D-plane (thus with no interaction forces between them) and play a Prisoner's Dilemma with their closest neighbors at each time step. They found that high velocities are detrimental to the evolution of cooperation, as the neighborhood of each particle then resembles a well-mixed population. The effect of velocity on the evolutionary dynamics is even more close to our model when the game is changed to a PGG, showing a similar rise-and-fall pattern (Cardillo et al., 2012).

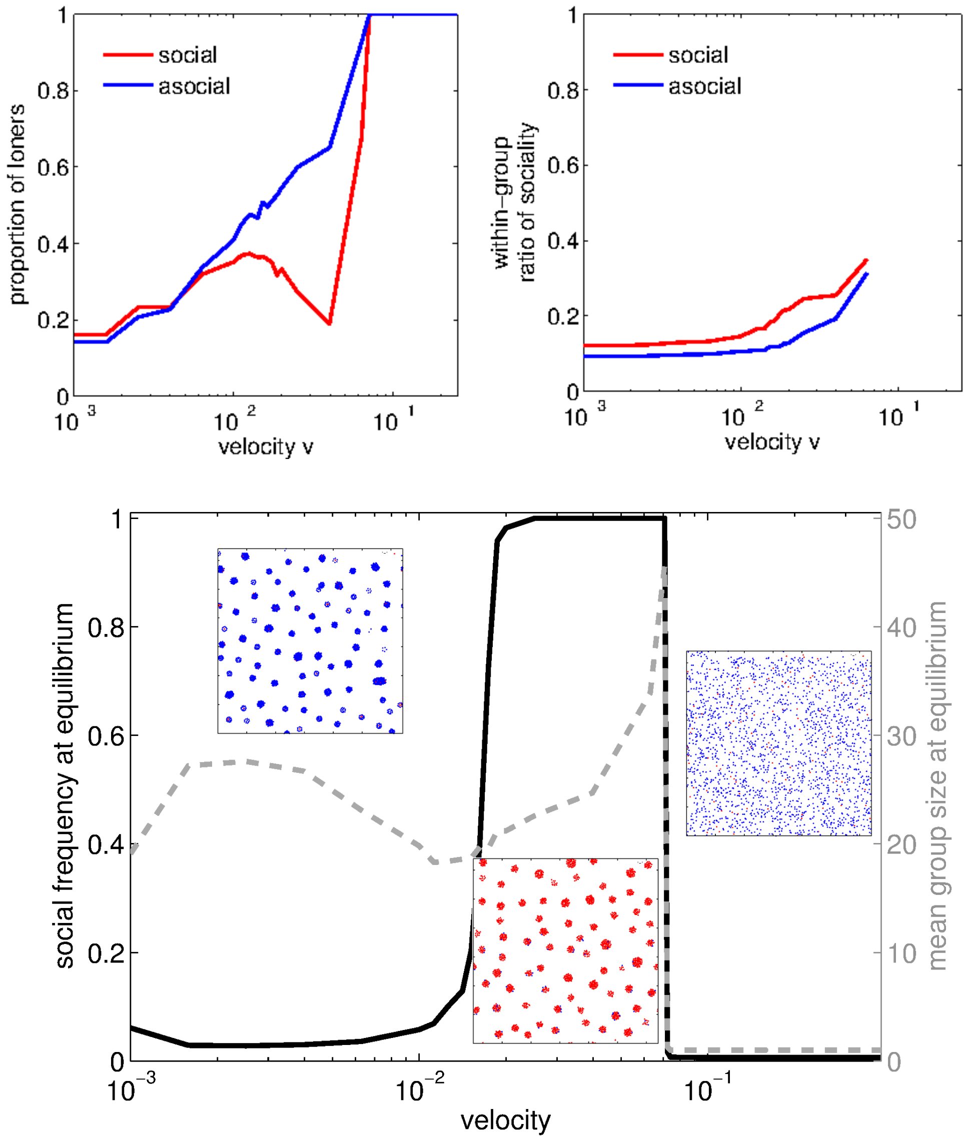

Figure 3.6: Effect of velocity on u_S, u_A, R_S and R_A and on the evolutionary equilibria

Top: proportions of ungrouped individuals increase with velocity, as it makes the influence of adhesion forces comparatively less important. At some point velocity has a beneficial effect on **S**s grouping as it allows them to explore their surroundings more in search of a group; however it does not for **A**s and $u_S < u_A$, until high velocities disrupt everyone's aggregation tendencies. Social ratio R_S in **S**s is slightly higher than R_A in **A**s. *Bottom*: Evolutionary endpoints when the velocity v varies. Three phases can be observed: for small v, particles form groups that are poorly assorted between **S**s and **A**s, so that sociality is not profitable enough to offset its cost: **A** players dominate at the evolutionary equilibrium; for intermediate v, groups are more volatile and sufficient assortment between **S**s occurs to promote sociality: **S** players dominate at the evolutionary equilibrium; for high v, individuals are not able to aggregate anymore and sociality is no longer profitable: the final state is a dispersed, asocial population. Insets: snapshots of the population after the aggregation step ($t = t_f$) at the evolutionary equilibrium. Parameters: $N_{pop} = 2048, L = 32.0, x_0 = 0.05, r_1 = 1.0, r_0 = 0.2, f_1 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 1.8, \beta_{aa} = 1.2, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, \eta = 0.3, b/c = 20$

Interaction radius: The same two transitions are observed when the interaction radius is changed (Fig. 3.7). When r_1 is low, particles are not able to form clusters: each particle's neighborhood is too small for cohesion to overcome diffusion and the population remains in the gas state. The transition to a fully social evolutionary equilibrium is concomitant with the appearance of groups. When r_1 increases, particles experience more populated neighborhoods and the resulting forces exerted on them are sufficient to compensate for **S** particles', but not **A** particles', diffusion. For still higher interaction radii, particles tend to stick to the group they initially belong to, and volatility remains low, so that assortment is closer to random. In the end, sociality is no longer profitable and vanishes. Whatever the winning strategy, the average group size in the population keeps increasing as the interaction radius becomes larger.

It appears that both short-range and long-range interactions are detrimental to the advent of sociality. Similarly to the case of the velocity, the interaction radius must belong to an intermediate range so that the **S** strategy is sufficiently assorted to be selectively advantaged.

Density: Here again, we observe a rise and fall pattern of the social frequency at equilibrium as a function of the population density $\rho = N_{pop}/L^2$ (Fig. 3.8). When density is too low, particles are too distant to form clusters within time t_f, so that **A** particles are favored and take over the population. When density is too high, particles are close to one another and very few of them are left alone, decreasing the effect of differential volatility, hence favoring **A** particles anew. Sociality can only invade the population when density is restricted to an intermediate range. Outside this range, either the absence of groups or the intensity of the competition favors the less costly type. A similar result has been found by Meloni et al. (2009) with a different model for individual motion and social game.

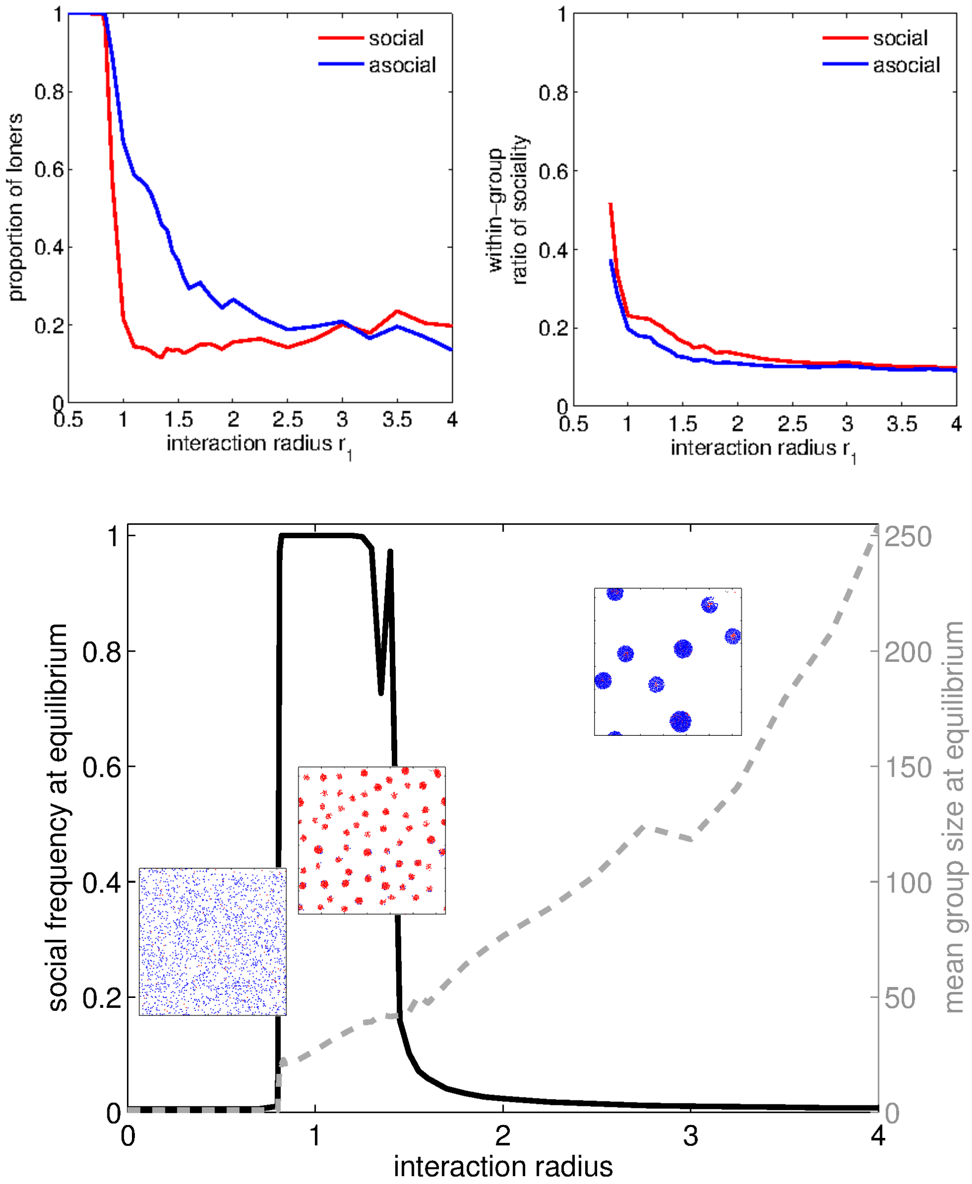

Figure 3.7: Effect of the interaction radius on u_S, u_A, R_S and R_A and on the evolutionary equilibria

Top: when r_1 is too low, particles do not have time to get in contact with one another and $u_S = u_A = 1$; when it increases, the proportions of ungrouped particles falls and $u_S > u_A$ throughout thanks to enhanced adhesion forces. *Bottom:* Evolutionary endpoints when the interaction radius r_1 varies. Three phases can be observed: for small r_1, particles do not manage to form any group and asociality takes over the population; for intermediate r_1, groups form such that differential volatility + assortment of **S**s combined favor sociality until invasion; for high r_1, interactions resemble that in well-mixed populations (so that assortment between **S**s is low) and very few individuals remain ungrouped (so that differential volatility is low), thus impeding the advent of sociality. Insets: representative snapshots of the population after the aggregation step ($t = t_f$) at the evolutionary equilibrium. Parameters: $N_{pop} = 2048, L = 32.0, x_0 = 0.05, v = 0.05, r_0 = 0.2, f_1 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 1.8, \beta_{aa} = 1.2, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, \eta = 0.3, b/c = 20$

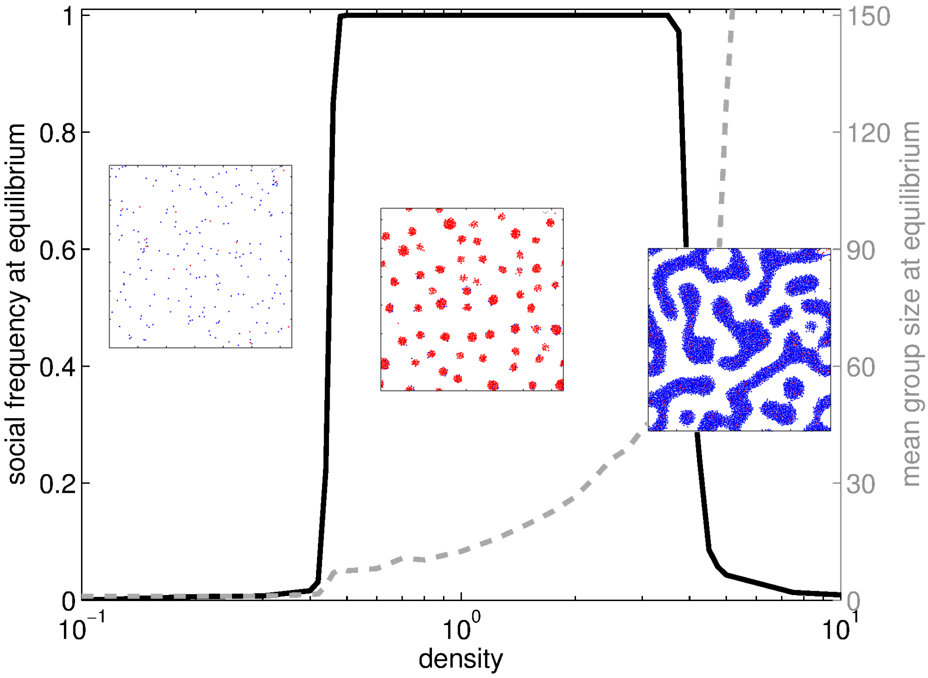

Figure 3.8: Effect of density on the evolutionary equilibria

Evolutionary endpoints when the density ρ varies. Three phases can be observed: for small ρ, particles are to dispersed for interaction forces to overcome directed motions so that no group forms and asociality dominates; for intermediate ρ, groups form such that differential volatility + assortment of **S**s combined favor sociality until invasion; for high ρ, interactions resemble that in well-mixed populations (so that assortment between **S**s is low) and very few individuals remain ungrouped (so that differential volatility is low), thus impeding the advent of sociality. Insets: snapshots of the population after the aggregation step ($t = t_f$) at the evolutionary equilibrium. Parameters: $L = 32.0, x_0 = 0.05, v = 0.05, r_1 = 1.0, r_0 = 0.2, f_1 = 5 \cdot 10^{-3}, \alpha = 1.0, \beta_{ss} = 1.8, \beta_{aa} = 1.2, \beta_{as} = \sqrt{\beta_{ss}\beta_{aa}}, \eta = 0.3, b/c = 20$

3.4 Discussion

3.4.1 Evolution of sociality via differential adhesion

The evolution of social behavior is a riddle for evolutionary biology because of the disruptive power of within-group competition between individuals that invest or not in the public good. In microbes and in the early stages of the transition to multicellularity, most mechanisms that sustain coperation through the use of cognitive abilities are ruled out. On the other hand, genetic relatedness may not be the only driver of the evolution of collective behavior, since microbial aggregates are commonly observed even when cells of potentially different origin come together. Here, I have explored one possible mechanism that allows the evolution of sociality and sizeable groups, when sticky self-propelled particles moving on a plane are assigned a fitness that depends on their social environment. The emergent structure of the population, underpinned by the adhesion forces between particles, feeds back onto the evolutionary dynamics of more or less adhesive types. By analyzing a model with successive cycles of aggregation-reproduction-dispersal, I have shown that sociality gets established in a limited range of parameter values: intermediate particle velocities; intermediate interaction radii; sufficient persistence in the particle directed movement; intermediate densities. These results can be understood in terms of two features of the population structure: assortment within groups and volatility, both of which affect the average fitness of particles with different interaction forces.

3.4.2 Strategy assortment and differential volatility

Assortment among types has long been pointed out as a requirement for the evolution of costly cooperative behaviors (e.g. Wilson and Dugatkin (1997); Fletcher and Zwick (2006); Fletcher and Doebeli (2009)). However, experimentalists as well as theorists still debate on how such assortment is actually reached when genetic relatedness does not appear to play a central role..

Most solutions involve some kind of recognition of other individuals' strategies, or at least information about a variable correlated with the strategy: a "green beard" gene coding for both the character, the recognition of copies of the genes among partners and preferential interaction with their carriers (Dawkins, 1976); partner choice (Kun et al., 2010; André and Baumard, 2011); conditional strategies involving choosiness (McNamara et al., 2008); matching by group size preference (Powers et al., 2011); direct (Trivers, 1971; Axelrod, 1984) or indirect/generalized reciprocation (Nowak and Sigmund, 1998; Wedekind and Milinski, 2000; Pfeiffer et al., 2005), etc. Here, I describe a mechanistic process by which particles are endowed with attractive forces that are independent of the social context. Assortment occurs with no need to assume that **S** particles attach *preferentially* with other **S**s; only *differential* attachment of **S**s and **A**s is required. This important distinction has been alluded to or stressed in several recent works (Smukalla et al., 2008; Strassmann et al., 2011; Garcia and De Monte, 2013). Ultimately, **S** particles enjoy the advantages of group cohesion to a larger extent, to the point that they can offset the cost of sociality.

Volatility is a much more neglected factor to achieve distinct reproductive successes for each type. Differential volatility means that asocials are less prone to be in a group, or at least more loosely stuck to the group ; therefore, more likely to get no group benefits or a lesser share of them. Surprisingly, the possibility that individuals do not participate in any group has been overlooked in models of the evolution of cooperation. In the papers that did, being alone results either from an encoded strategy, (e.g. Hauert et al. (2002a,b)), or to coercion by cooperators (Sasaki and Uchida., 2013), rather than being a by-product of an explicit group formation process. Recently, detailed models of motion began to be implemented in evolutionary models that allow in principle for the existence of lonely individuals (Meloni et al., 2009; Cardillo et al., 2012). Indeed, in many actual group-structured biological populations, a proportion of individuals typically fail to join any group (Smukalla et al., 2008; Dubravcic et al., submitted). We stress that, as soon as the proportion of ungrouped particles differ for both types, the evolutionary dynamics is affected in favor of the more strongly aggregating type. In our model, differential volatility occurs as the cooperative trait is related to grouping ability itself, as stronger adhesion forces confer cohesiveness to groups but also enhance individual attachment. Any cooperative trait increasing the probability to end up in a group would yield qualitatively similar results: socials and asocials may be defined on the basis of differences in properties other than attachment, e.g. their interaction radius.

In general, assortment and volatility are not independent features of the emergent population structure. In our simulations, the faculty for **S** particles to become positively assorted comes along with a lesser tendency to be left alone by the aggregation process. However, it is noteworthy that, in situations when sociality is the winning strategy, positive assortment alone may not be sufficient to account for its advantage. Indeed, assuming that $R_S > R_A$ and $u_S < u_A$, the two conditions 1) $b\,R_S - c + b\sum d_S(n)/n < b\,R_A$ (assortment alone is not enough to favor sociality) and 2) $b\,R_S\,(1-u_S) + b\sum d_S(n)/n - c > b\,R_A\,(1-u_A)$ (assortment + differential volatility combined favor sociality) are compatible as soon as $R_A\,u_A > R_S\,u_S$. In this case, differential volatility drives the rise in frequency of sociality, while it would not be the case discounting singletons. This suggests that in real settings where group size is distributed and not fixed, models and experiments might overestimate the constraints for cooperative behavior to be favored. While positive assortment and differential volatility are two complementary effects that promote sociality, they both stem from the biologically plausible hypothesis that a character may affect the expected group size distribution. Examples of traits regulating group size are known in *D. discoideum* (Roisin-Bouffay et al., 2000; Golé et al., 2011), although their effects on the group size distribution have to my knowledge never been quantified.

3.4.3 Role of group formation

I highlighted that parameters related to particle motion are key in the evolutionary success of social individuals. Noise, velocity, density and interaction radius must be restricted to specific ranges for sociality to be able to take over the population; otherwise asociality dominates. In actual biological settings, these parameters might have co-evolved with adhesion properties, and their evolutionary dynamics may be explored with a multi-trait model.

This model stresses that observing and quantifying the properties of the population structure generated by a given mixture of strains may inform on the mechanisms that underlie the evolutionary process. The issue of being able to count a large amount of aggregates (so that statistics are reliable) can be overcome by means of microscopes screening a large surface and still maintaining a single-cell resolution (Houchmandzadeh, 2008; Dubravcic et al., submitted). The analysis performed in section 3.3.3 indicates what are the expected patterns if evolutionary experiments are carried out under different environmental conditions that affect cell-level properties, such as cell density or substrate hardness (that conditions cell movement). More importantly, they indicate two statistics that may predict if a given population would evolve towards more or less sociality.

3.4.4 Conclusion

Although unicellular organisms are often found in large aggregates, their high dispersal abilities and the consequent mixing of genotypes makes the establishment and maintenance of social behavior aparently paradoxical. When physical mechanisms underlying the formation of groups are made explicit however, the evolution of sociality looks less mysterious, and one can start asking quantitative questions on the processes that led to the emergence of cellular aggregates. The simple model presented here can be enriched with further details implementing additional features of microbial organisms, such as alignment terms (Vicsek et al., 1995; Grégoire et Chaté, 2004), an explicit account of the cell shape (Peruani et al., 2012) and chemotaxis (Jiang et al., 1998; Calovi et al., 2010). The exploration of the mechanistic role of cell-cell interaction terms in shaping the social structure is a fundamental step to understand altruism in microbes, as well as the possible evolutionary paths towards multicellularity.

3.5 Effect of ecological vs. evolutionary time scale

This section is very much a work in progress; more simulations and analyses are required to confirm the exposed results. However, I believe it already displays some interesting features on conflicting levels of selection and group dynamics.

3.5.1 Hypotheses

Until now, the impact of natural selection on the composition of the population was deemed to occur on timescales much longer than that of group formation: individuals were let the time to swarm before a reproduction event occurs, and re-dispersed afterwards. This setting is mostly relevant for microorganisms such as Myxobacteria or social amoeba that alternate a phase of aggregation triggered by the depletion of nutrients in the environment with a sporulating phase where a proportion of the population is able to disperse and colonize a new environment. However, other microorganisms divide while they forage (Nadell et al., 2010; Simon et al., 2012). Let us consider that reproductive events are periodic. We denote t_R the period between two successive reproductive events. At each time step, the payoff of each individual is calculated according to a PGG in its current group (if any). Every t_R time steps, the cumulated payoff of the last t_R time steps is used to define an individual's probability to leave offspring. Offsprings appear just next to their ancestors (at a distance $2r_0$), in a random orientation. To isolate the role of the interplay of time scales from that of varying population densities on evolutionary dynamics (Sanchez and Gore, 2013), the total population size is still kept constant : each time a offspring appears, an individual is chosen at random to die. Therefore, groups dynamically grow or shrink due to internal reproductive dynamics and the two conflicting levels of selection are immediately apparent in simulations: **S** individuals are disadvantaged compared to **A** individuals in their own groups but groups comprised of many **S** individuals yield more benefits and thus expand more (see Box 2.4.).

3.5.2 Evolutionary trajectories

In Figure 3.9, the population begins to form clusters on a fast time scale ($t = 100 \sim 200$). Among them, groups of a few **S**s emerge by chance ($t = 300$) and grow more rapidly than groups composed mostly of **A**s. However, as soon as they merge with nearby mostly-**A** groups or free **A**s are attracted by them ($t = 400$), intra-group competition occurs while they keep on expanding ($t = 500$). When these group are marred by too many **A**s, they cannot compete against newly formed mostly-**S** groups ($t = 800$) and collapse ($t = 900 \sim 1000$). In the end, many **A**s die and the social frequency in the population increases. A contradiction seems to arise: when there remains only one group in the population, how come this group is not invaded by the few **A**s left until they take over? The maintenance of sociality relies on two mechanisms: 1) as, unlike mostly-**S** groups that are very cohesive, mostly-**A** groups are more volatile, the proliferation of **A** individuals would make the group split in several parts and re-generate group competition. However, this does not even happen in practice as 2) **A**s at the border actually do not belong to the group according to the criterion used, as they are not "stuck" to it like a solid but circulate like a liquid around its surface. Therefore, even though in-group **A**s have a payoff advantage relative to in-group **S**s, it is compensated on average by these free **A** individuals that earn nothing from the group, thus dying quickly and being replaced at the periphery by volatile, formerly in-group **A**s. Thanks to this, once a high level of sociality is reached it is generally very resistant to a novel exploitation by asocials, as confirmed qualitatively by simulations.

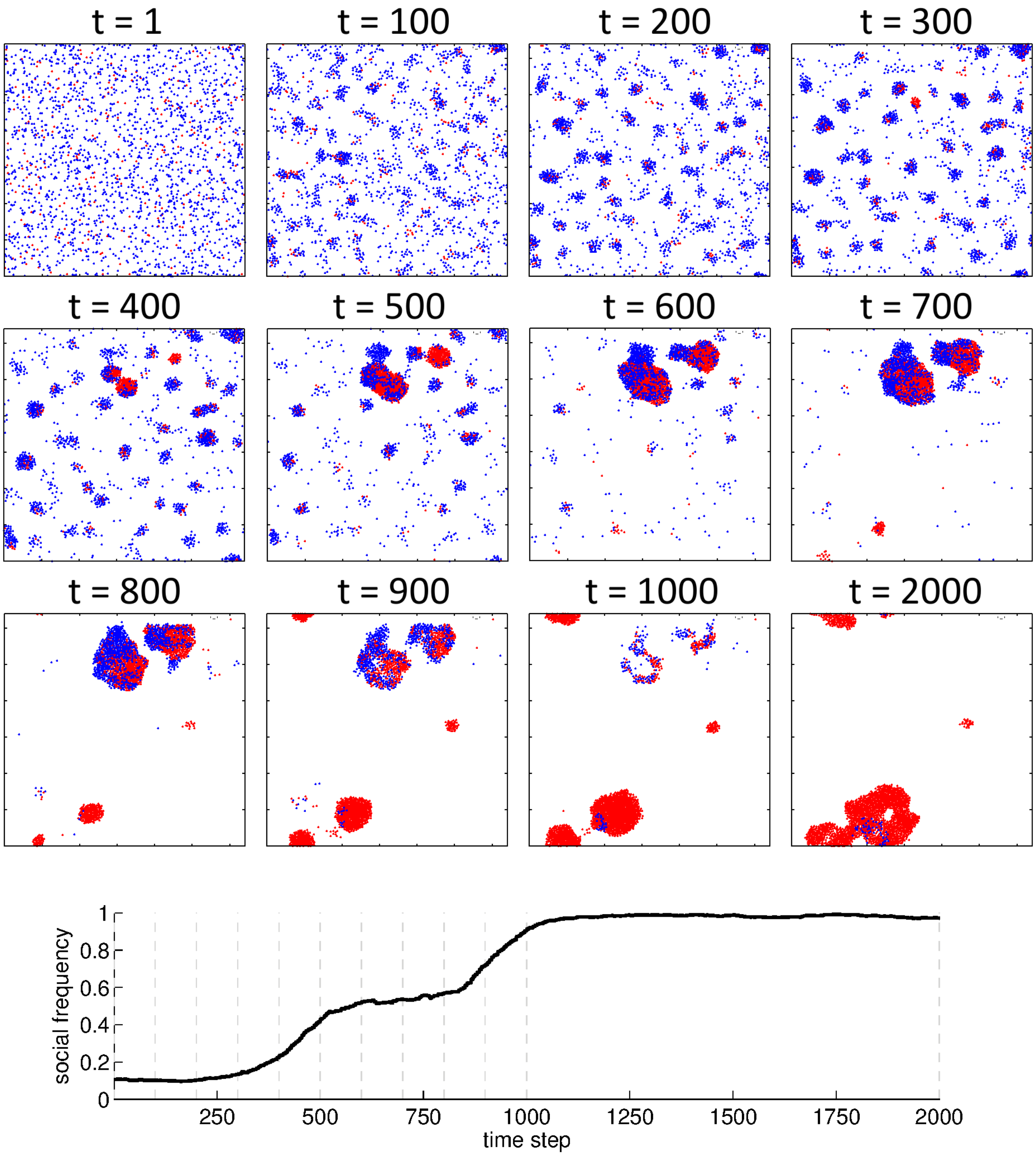

Figure 3.9: Snapshots of an evolutionary trajectory with motion and reproduction concomitant: case when **S**s dominate

The population is represented at distinct instants of the evolutionary trajectory. The bottom panel displays the variation of social frequency in time. See explanations in the main text. Parameters: $N_{pop} = 2048$, $L = 32.0$, $v = 0.05$, $x_0 = 0.1$, $r_1 = 1.0$, $r_0 = 0.2$, $\pi_{ss} = 1.8$, $\pi_{aa} = 1.2$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $f_1 = -f_0 = 5 \cdot 10^{-3}$, $\eta = 0.3$, $b/c = 20$, $t_R = 5$. There are no mutations.

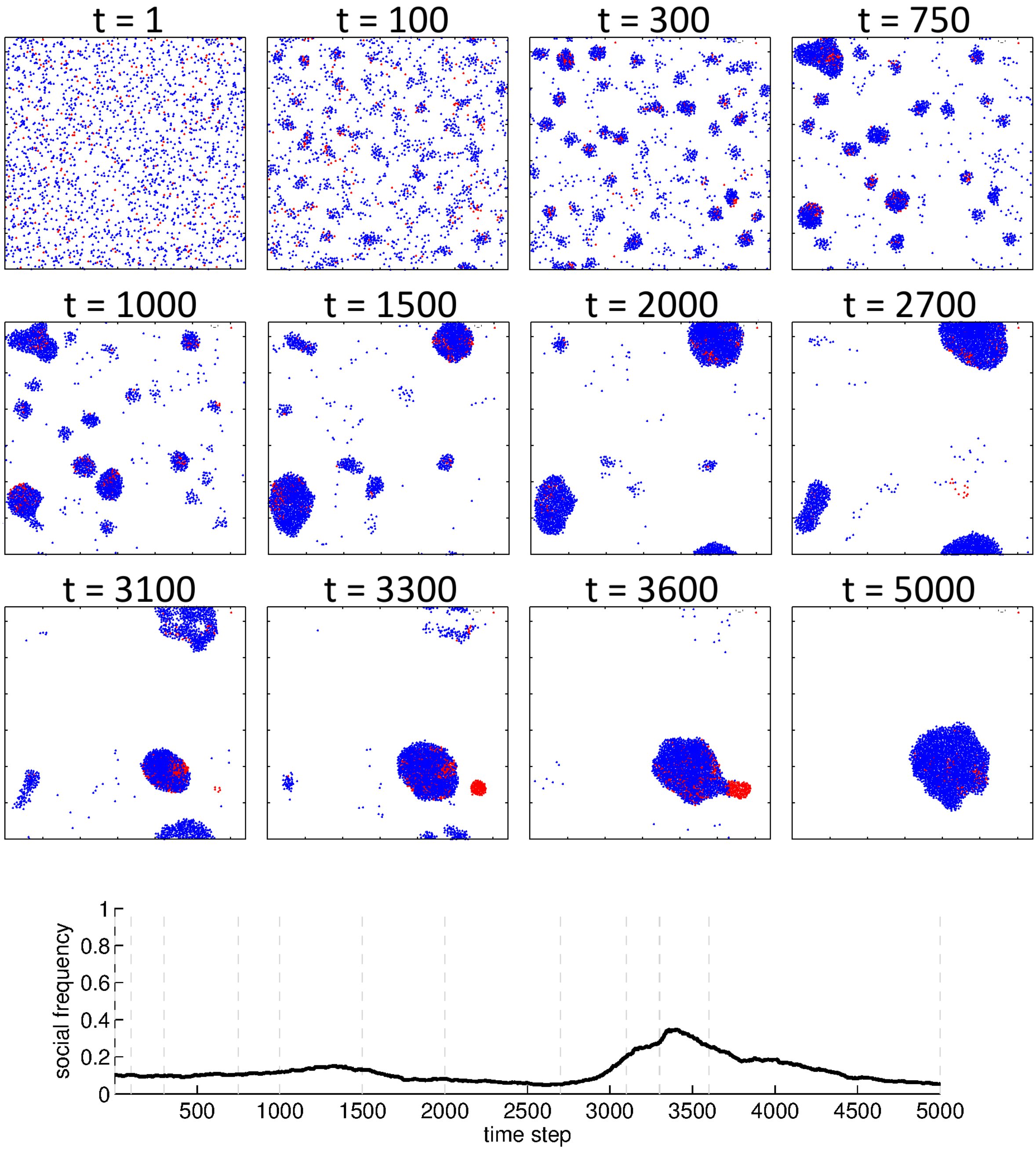

Figure 3.10: Snapshots of an evolutionary trajectory with motion and reproduction concomitant: case when **A**s dominate

The population is represented at distinct instants of the evolutionary trajectory. The bottom panel displays the variation of social frequency in time. See explanations in the main text. Parameters: $N_{pop} = 2048$, $L = 32.0$, $v = 0.05$, $x_0 = 0.1$, $r_1 = 1.0$, $r_0 = 0.2$, $\pi_{ss} = 1.8$, $\pi_{aa} = 1.2$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $f_1 = -f_0 = 5 \cdot 10^{-3}$, $\eta = 0.3$, $b/c = 10$, $t_R = 5$. There are no mutations.

What also appears in simulations, and needs to be quantified further, is that such robustness of sociality when very few groups remain requires **S** players to have reached a critical mass and a critical fraction in their respective groups, as pointed out in a different way in a non-spatially explicit model where groups form randomly and are let evolve for a fixed amount of time (Cremer et al., 2012). In Figure 3.10, b/c has been decreased. Despite forming a promising small group at $t = 2700$, **S**s soon do not manage to dominate their group even though they make it grow rapidly. Between $t = 3300$ and $t = 5000$, the fusion of a solid all-**S** group with a much larger mostly-**A** group proves lethal to the former, impeding the takeover of sociality. In this simulation, the evolution of the social trait in future times is probably doomed: to happen, it would require *S* individuals to form a cluster far enough from the gigantic A-group so as to outcompete it and not be "phagocyted" by it; but it seems impossible as individuals are born close to their ancestor.

In some cases, the dynamics of the social trait for a given set of parameters result in either full invasion or full extinction depending of its initial frequency (Fig. 3.11; here, social and asocial interaction forces are more distant from each other than formerly). Such bistability (akin to what is predicted by, for instance, a Stag Hunt game) results from **S** players being able or not to form small clusters locally that are immune to asocial exploitation for a sufficient amount of time. Unlike for instance in Figure 3.10, once sociality is triggered it generally does not falls back; conversely, when sociality becomes too scarce it cannot recover. A wide parameter exploration would be needed to assess the influence of microscopic parameters on the evolutionary outcome, and "map" the (possibly) different dynamics (directed, bistable, polymorphic, etc.) on the parameter space, but it is out of the scope of this thesis.

3.5.3 Effect of the generation time

To analyze the influence of the discrepancy between the ecological and evolutionary time scales, I performed repeated evolutionary simulations for different values of t_R and computed the average final social frequency. Figure 3.12 suggests that concomitant ecological and evolutionary

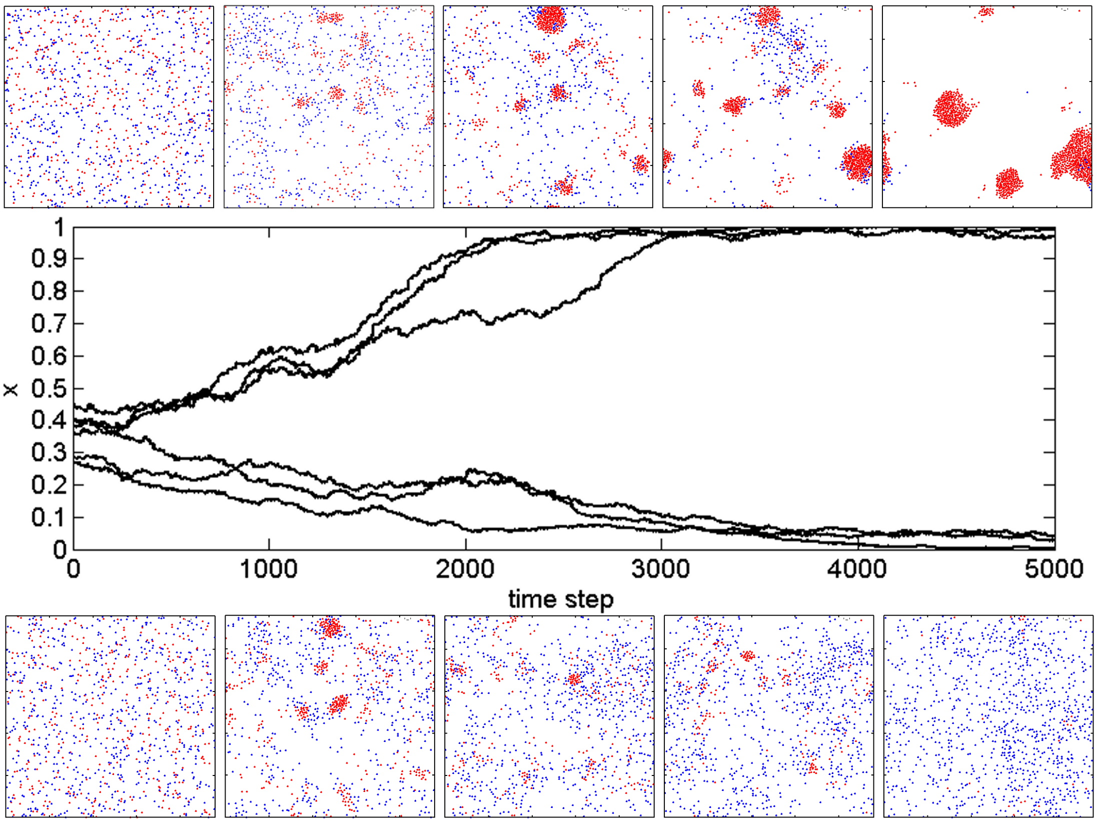

Figure 3.11: Example of bistable equilibrium when the evolutionary and ecological time scales are no longer separated.

Central panel: several evolutionary trajectories are shown, starting from diverse social frequencies x_0 lying either side of a threshold frequency $x^* \sim 0.36$. When $x_0 < x^*$, sociality cannot reach the necessary "local critical mass" to outgrow asociality, and decreases in frequency until near-extinction (bottom panel, with snapshots of a representative dynamics at distinct points in time). Conversely, when $x_0 > x^*$, sociality quickly manages to find its way forming small clusters dense enough in **S** players to expand despite the local exploitation of **A** players. In the end, sociality reaches near-fixation (top panel, with snapshots of a representative dynamics at distinct points in time). Parameter values: $L = 24, N_{pop} = 1024, v = 0.05, r_1 = 0.8, r_0 = 0.2, f_1 = -f_0 = 5 \cdot 10^{-3}, \beta_{SS} = 1.8, \beta_{AA} = 0.5, \beta_{AS} = \sqrt{\beta_{SS}\beta_{AA}}, \eta = 0.3, b/C = 5, t_R = 10,$ 5000 time steps.

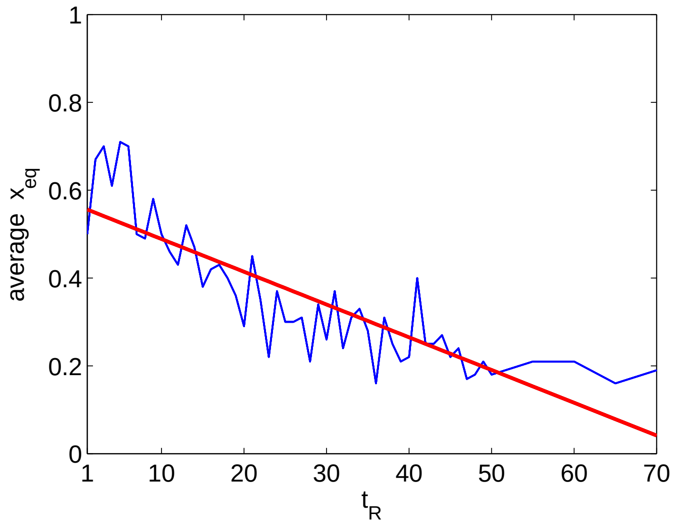

Figure 3.12: Effect of the generation time t_R on the average equilibrium frequency of **S** players.

Although dynamics are highly variable given a set of parameters and a generation time t_R, mean values of the social frequency at equilibrium appear to decrease with t_R. This can be accounted by the decreased ability for **S** players to form quickly expanding clusters that are robust against the exploitation of **A**s when reproduction is slow relative to motion, thus enabling **A**s to join and mar newborn social groups. Parameters:

time scales (i.e., frequent reproductive events during motion) makes it easier for high levels of sociality to arise in populations.

Recently, Cremer et al. (2012) published a model that bears conceptual similarities to this one. Individuals undergo lifecycles characterized by 1) a phase of group formation in which separate groups of fixed size are formed by an unbiased stochastic process; 2) a phase of group evolution in which groups evolve separately for a fixed "regrouping time". Highly cooperative groups yield higher benefits and reach larger carrying capacities, but internal competition advantages defectors; 3) a phase of re-merging of groups into a global pool. In their model, short regrouping times favor the evolution of cooperation until fixation; intermediate regrouping times favor coexistence between cooperators and defectors; and high regrouping times favor bistability between full cooperation and full defection (Fig. 3.13). Again, a more thorough look on simulation data will be required to compare further my preliminary results with Cremer et al.'s.

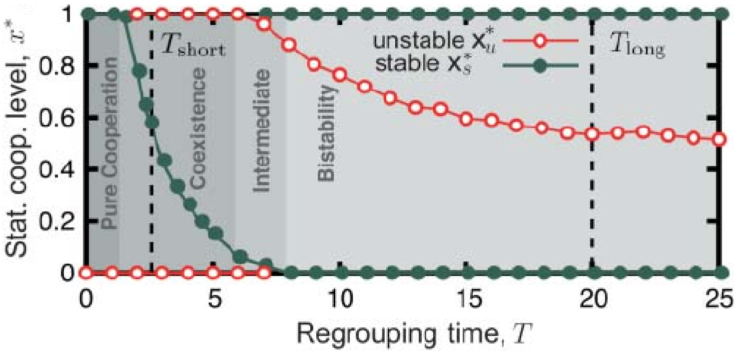

Figure 3.13: Evolutionary fate of the cooperative trait in Cremer et al.'s model, as a function of regrouping time T

When regrouping time T is high, a *group-fixation mechanism* (i.e., higher carrying capacities achieved by purely cooperative groups) leads to bistability. When T is decreased, a *group-growth mechanism* (i.e., groups with many cooperators growing more rapidly) becomes more prominent and generates coexistence between cooperators and defectors. When T is much larger than the selection time $= 1/(\text{selection strength})$, cooperation manages to take over the population. Figure taken from Cremer et al. (2012); see also discussion therein.

3.5.4 Conclusion: role of time scales

This extension of the model presented in section 3.2 allows to overcome the assumption that groups are re-dispersed at each generation in a global pool before undergoing a novel cycle of aggregation. First results suggest that relaxing this assumption – letting individuals reproduce and die along with the group formation process and groups endure across generations – enhances the ability of the social trait to increase in the population, as quick growing of successful (i.e., dominated by **S** players) groups helped hinder the local disadvantage **S** individuals have within their groups. This is very much in line with past work where groups are authorized to last several generations, a mechanism suitable for promoting cooperative traits (Fletcher and Zwick, 2004; Killingback et al., 2006; Traulsen and Nowak, 2006). However, much richer dynamics are possible than in such theoretical works, as groups are no longer separated once and for all, and the notion of belonging to one group rather than another is more fluid. Here, clusters can potentially merge, split, grow or shrink, owing to both collective motion dynamics (the SPP) and birth/death processes (ruled by the PGG) at the individual level. While these two processes have been well studied in the literature, to my knowledge their combined effect in the context of social dilemmas has not been addressed so far. Although groups are not allowed to reproduce or die by themselves, this model could be interpreted in the framework of recent theoretical works attempting to solve the puzzle of multilevel selection (Simon et al., 2012).

Chapter 4

Conclusion

4.1 Main results

In this section are summarized the main conclusions and issues that I judge noteworthy of discussion.

Costly sociality can evolve via blind assortment, even when altruistic. In this manuscript, I focused on the basic requirements for primitive collective lifestyle. In the literature, one can notice an ongoing trend to explain cooperation by assuming the pre-existence of very elaborate individual behaviors in more or less explicit ways. Sometimes, a combination of several cognitively demanding or socially acquired abilities (e.g. memory, peer recognition, conditional behavior, obedience to a norm, risk aversion, etc.) is invoked. While such assumptions are plausible in rational, socially-driven humans, they fall short in providing real insight on the ubiquity and diversity of sociality as evidenced in recent years in very simple, e.g. microbial, species. Second, most of these models put the emphasis on helping / sharing behavior in settings where individuals do interact and form groups, but elude the issue of how individual traits generating and sustaining such groups can emerge. As this is the basic brick for the ulterior evolution of more complex interactions, it must be accounted for with minimal hypotheses on the social context.

In chapter 2, I show that a costly, genetically encoded trait that increases its carrier's propensity to form groups (by any mechanism), and benefits to other group members owing to enhanced cohesion, can emerge and expand in a biological population. Social individuals thrive because they manage to get assorted together, i.e. the average social individual experiences more social groups than the average asocial individual. Additionally, socials end up ungrouped less often than asocials. Positive assortment of social individuals occurs without them being able to recognize one another, or interact preferentially. This is of particular importance to account for sociality in microbes, as it keeps the cognitive requirements as minimal as possible: *differential attachment* in both types (social and asocial) is sufficient with no need of *preferential attachment*, thus providing a parcimonious scenario for the evolution of grouping traits in microbes.

In what was at first a thought experiment, Dawkins (1976) imagined the evolutionary consequences of a "green beard" gene (or set of linked genes), defined as a gene encoding three behaviors: 1) a phenotypic tag (the "green beard"); 2) the ability to recognize other carriers of the tag; 3) a cooperative behavior preferentially directed toward them. Green beard genes were considered improbable until several presumed examples of such genes were reported in the literature (Keller and Ross, 1998; Ponte et al., 1998; Riley and Wertz, 2002; Gibbs et al., 2008; Smukalla et al., 2008). In two recent papers, Gardner and West re-phrased the definition of green beards as traits that are cooperative (resp. spiteful) and entail assortment with other carriers (resp. noncarriers).This re-definition is however misleading compared to the initial formulation by Dawkins as it leaves behind the notion of *preferential interaction*; moreover, it focuses on dyadic interactions, whereas N-player interactions cannot be formally reduced to those.

In chapter 2, **S** individuals do not interact *preferentially* with other **S**s, compared to **A**s themselves; but assortment happens to emerge all the same as **S** individuals interact more, as a whole.

Biased interactions are a ultimate effect rather than a proximate cause (Nowak et al., 2010a). Neglecting such possibility, Gardner and West treated *preferential* and *differential* interaction as equal and coined any cooperative behavior that entails assortment at a single locus a "green beard" trait, while it is not necessarily so according to the original definition. Combined with the widespread intuition that green beards are rare in nature, such confusion in terms might let one think that assortment at a single locus itself is dubious, and that assortment on the whole genome (i.e., kin selection) is the process *par excellence* to promote cooperative behavior. Actually, many distinct mechanisms can lead to assortment in otherwise unrelated individuals.

The altruistic / directly beneficial status of a social trait depends on the population structure. The evolution of a costly cooperative trait is only paradoxical if the cost incurred by the carrier is not canceled by compensatory direct benefits. Consequently, a whole family of models describes mechanisms that, at some point, "relieve the dilemma". In the PGG framework, this can be achieved by reducing the size of the group, as the direct benefit accrued by a cooperator is b/N, e.g. considering lonely individuals that do not participate to the game (Hauert et al., 2002a,b), allowing multigenerational (Fletcher and Zwick, 2004; Killingback et al., 2006), even splitting (Traulsen and Nowak, 2006) groups, or letting group size preference co-evolve with cooperation, and individuals group with those matching their preference (Avilés, 2002; Powers et al., 2011), etc. In these settings, cooperation might be altruistic at some point when groups are large, then become directly beneficial because of the large-size group depletion subsequent to free-riders exploitation. In chapter 2, I stress that the benefit-to-cost ratio conditions not only the evolutionary fate of the social trait (in the toy model, either fixation or extinction), but also its "status" throughout the evolutionary trajectory. When socials are rare, groups are still small and sociality can increase in frequency via direct benefits. Once the social trait reaches a threshold frequency, it keeps on spreading until fixation thanks to positive assortment even though the social trait has become altruistic in the meantime.

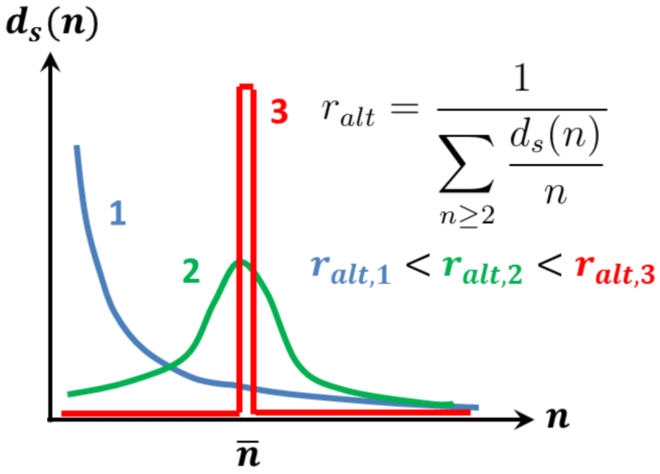

Figure 4.1: Effect of the group size distribution on the maximal benefit-to-cost ratio for altruism

At unchanged average group size $\bar{n}$, the maximal benefit-tot-cost ratio for which cooperation is altruistic is lower when group size is distributed (cases 1 and 2) than when group size is fixed (case 3), and cooperation can evolve more easily via direct benefits. If the group size distribution is skewed in favor of small groups (case 1), this effect is enhanced compared to a centered distribution (case 2) as direct benefits are greater in small groups.

Also noteworthy is the influence of group size distributions on the status of a social trait; when group size can vary, the condition for a trait to be altruistic is expressed as a function of the group size distribution $d_s(n)$ experienced by a social individual:

$$b/c < r_{alt} = \frac{1}{\sum_{n\geq 2} \frac{d_s(n)}{n}}$$

At fixed mean value $\bar{n} = \sum n\, d_s(n)$, the condition for altruism is therefore more or less stringent depending on the shape of the distribution, as shown in Figure 4.1. In particular, a trait that is altruistic when group size is fixed can be directly beneficial is group size is variable, and even more id group size distribution is skewed toward small groups.

Sociality naturally gets coupled with cooperation for group cohesion during the in-group phase. In section 2.4, I modeled the case when the assumption on the coupling of stickiness in the aggregation phase and cooperation in the in-group phase is relaxed. This corresponds to situations when a cell is genetically programmed to, for instance, secrete adhesive substances during the former phase and refrain doing so during the latter. I assume that such a switching behavior entails an additional cost, e.g. imposed by a quorum-sensing ability to detect the beginning of the in-group phase and halt or trigger the cellular machinery consequently, whereas non-switching strategies do not need such ability. I show that, for a very large portion of the parameters ranges, switching strategies are eliminated, so that the only viable strategies are to be either social or asocial all along the life cycle. The argument actually works even for null additional regulatory cost: indeed, when **SC**s (sticky cooperators) are not able to outcompete **SD**s (sticky defectors), **AD**s (non-sticky defectors) outcompete both anyway.

A minimal initial amount of sociality is required. The 2-strategy model is based on the assumption that the social trait can take up discrete values, such that pro-social mutations encode for a specific function that discontinuously enhances the propensity to form groups. The continuous trait model rather assumes that such function pre-exist but is expressed at various levels. In both cases, a condition for an increase in sociality to be selected for is that a certain level of sociality is present in the population to begin with. The frequency of the social trait in the 2-strategy case, and the resident ability to interact in the continuous case, must overcome a threshold below which sociality is wiped away. As soon as this condition is met, sociality rises to its utmost level in the nonassortative case. The necessity of a minimal core of sociality to trigger its own evolution is a recurring pitfall in evolutionary models: for instance, in nonlinear games, an invasion threshold has to be reached to make cooperation increase and persist. Actual models often avoid the issue altogether, rather focusing on the less challenging puzzle of maintenance (e.g. initializing models with a 50-50 mixture of cooperators and cheaters). However, such con-

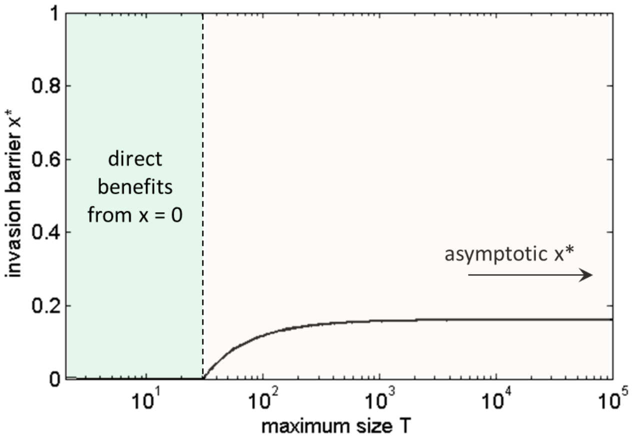

Figure 4.2: Invasion barrier required to trigger sociality, as a function of the patch size T.

When T is small, group sizes are small and the (here fixed) benefit-to-cost ratio warrants that sociality can evolve from scratch thanks to direct benefits. When T increases, an initial frequency x^* of socials is necessary, that does not exceed an asymptotic value < 1. Parameters: $b/c = 20$, $\pi_{ss} = 0.8$, $\pi_{aa} = 0.3$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$.

straint may not be as critical as one may think. In the aforementioned models, the thresholds are typically low and likely to be reached at some point in evolutionary history, especially when population sizes are locally small, hence subject to stochastic effects, and the mutation load is high. In simulations with finite-size populations, indeed, the onset of sociality is easier than predicted theoretically (Fig. 2.5)

Large groups do not prevent the evolution of sociality. Most models predict that large group sizes are doomed because of direct benefits decreasing to zero with group size, e.g. (Powers et al., 2011). In the toy model, the threshold required to trigger the invasion of sociality is bounded when the patch size T varies, so that, provided the asymptotic threshold is reached, sociality is in principle possible in groups of any size. This is good news with regard to microbes as some of them they tend to aggregate in a very large number (Tang et al., 2002; Smukalla et al., 2008).

The theoretical mechanism is compatible with explicit (realistic) aggregation models where the social trait encodes the intensity of adhesion forces. Chapter 2 provides an analytical argument for the evolution of social traits for a “black box” group formation process, as well as a proof of principle with a toy example; chapter 3 confirms that this result is compatible with a more realistic and spatially explicit aggregation scheme, serving as a validation of chapter 2. The self-propelled particles model used in this chapter is intended to be specific enough to draw precise conclusions on the effect of microscopic parameters on sociality, but generic enough to encapsulate zeroth-order behaviors of a wide range of species. The assumptions made (spatial extension of particles; interaction forces depending on their distance; inertia on movement) remain weak and are consistent with many empirical studies on microbial motion.

The evolution of sociality is only possible in specific conditions on ecological and microscopic parameters of motion. The coupling of the SPP aggregation model and the game-theoretical framework allows to "read" directly the conditions that are favorable to sociality upon the obtained ESSs . High noise (e.g. due to locally perturbed environments) – that brings particle movement closer to an unbiased Brownian motion –, low density, and high velocity / low interaction radius – that rather emphasize directed motion over attraction between particles – all mar individual clustering, hence sociality. High interaction radius and high density make individuals neighborhood close to well-mixed, and low velocity hinders sufficient mixing of individuals, thus thwarting the assortment of socials during the transient. As a result, intermediate values of the population density, particle velocity and interaction radius, and moderate noise are required for a social mutant strain to replace a resident asocial strain. I also stress that the success or not of the social trait can be derived from the knowledge of macroscopic observables on the population structure, namely:

- the average ratio of sociality experienced by the average social (resp. asocial) individual within its group. This quantifies the level of assortment of socials;
- the proportion of ungrouped individuals of each type.

Whereas positive assortment of socials within groups is a well-known determinant for their success, *differential volatility* (i.e., the difference in proportions of social and asocial individuals staying outside groups) is a neglected factor in the literature, although it is equally likely to boost sociality. This is because most models 1) consider group size constant, and no individual alone; 2) focus on helping traits that take place in pre-existing group structures.

The emergent population structure resembles that of real microbes. Chapter 3 evidences that with very simple assumption on particle movement (namely, volume exclusion and attraction until a cut-off radius), it is possible to generate aggregation patterns and population structures that are quite close to some encountered in real microbes (Fig. 4.3). For instance, in *Dictyostelium discoideum*, cells converge toward centers of attraction by relaying cAMP signals, resulting in local clusters of circular shape and comparable sizes (Fig. 4.3A). While several works describe more thoroughly group formation in Dicty – e.g. explicitly modeling chemotaxis (van Oss et al., 1996; Palsson and Othmer, 2000; Calovi et al., 2010) – and capture more exactly the features of the transient phase (for instance the spiral waves and star-shaped streams resulting from cAMP gradients – not shown here), the generic model I used still retains some of the main qualitative characteristics of aggregation. The ability to aggregate, and the sizes of the resulting groups depends on the intensity of the attachment force between mobile cells, which is consistent with what is experimentally observed in cells expressing adhesion protein on their membrane (Foty and Steinberg (2005), Fig. 4.3B).

Another striking feature of the model of chapter 3 is the spatial segregation occurring between sticky and less sticky cells, which is consistent with experiments on flocculating yeast and N-cadherin expressing L cells. In yeast, Smukalla et al. (2008) mixed wild-type cells endowed with a social gene FLO1, coding for the expression of an adhesion protein, with FLO1-knockout cells. They observed that 1) while groups contain cells of both types, FLO1$^-$ cells are under-represented in groups and make for most of the ungrouped cells; 2) within groups, FLO1$^-$ cells

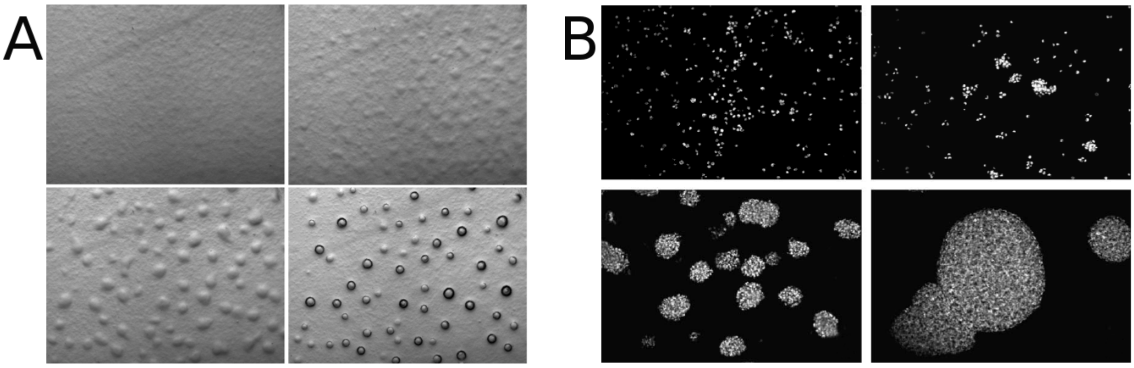

Figure 4.3: Formation of groups in *Dictyostelium discoideum* and in cadherin-expressing L cells

Panel A: Temporal snapshots of a group formation process in *Dictyostelium discoideum*: when starved, "pacemaker" cells secrete a cAMP signal that is relayed by successive waves to neighbors. Cells follow cAMP gradients until they gather into localized, circular-shaped aggregates of sizes of the same order of magnitude (not all cells enter an aggregate, though (Dubravcic et al., submitted)). Later on, they will form a mobile slug oriented by phototaxis and morph into a fruiting body whose spores are dispersed and stall cells die. Pictures produced by Darja Dubravcic. Panel B: Result of aggregations of N-cadherine-transfected L cell lines with increasing cadherin expressions levels. Cell aggregation rate increases with the level of expression of the adhesion protein. Reproduced from (Foty and Steinberg, 2005).

tend to occupy the outermost layer of the floc (Fig. 4.4A). Three years before, Foty and Steinberg (2005) reported a similar pattern in N-cadherin expressing L cells: they mixed strains that express distinct levels of the protein, and found out that low cadherin-level cells were relegated to the periphery of aggregates, with high cadherin-level cells clumped together within.

The rate of reproduction, relative with the time scale of motion, influence the evolutionary equilibrium. The preliminary results of the last section of chapter 3 seem to evidence that the interplay of reproduction and mobility may change drastically the evolutionary dynamics of the social trait, not only during the transient but also the evolutionary equilibrium itself. This is of interest for species whose life cycle, unlike Dictyostelids and Myxobacteria, is not separated in a group formation and a reproduction phases. The preliminary results shown in section 3.5 need however further work to assess accurately the effect of the concomitant (ecological and evolutionary) time scales, and the nature of equilibria that are expected (monomorphic or dimorphic; bistable or not) according to the reproduction time t_R.

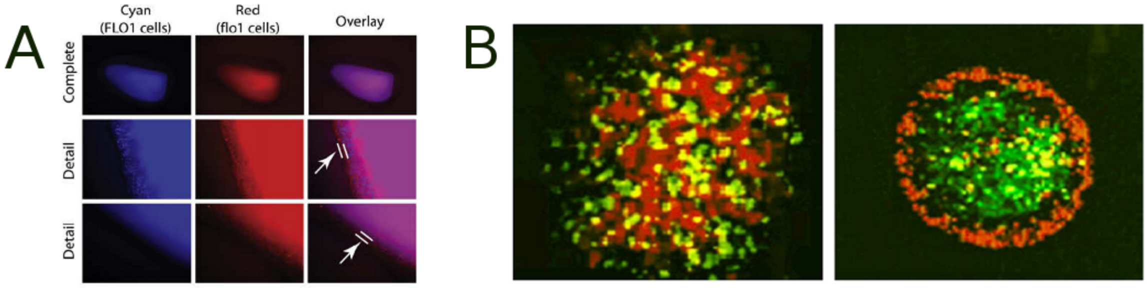

Figure 4.4: Spatial cell sorting in *S. cerevisiae* and in cadherin-expressing L cells

Panel A: in mixed cultures in budding yeast, flocculating cells endowed with the FLO1 gene occupy the core of aggregates and nonflocculating cells agglutinate at the periphery. Reproduced from (Smukalla et al., 2008). Panel B: two N-cad-transfected L cell clones expressing N-cad at their surfaces in the ratio of 2.4:1 are mixed in equal proportions and cultured as hanging drops. The first picture displays the inital cell mixture; after 24h of incubation, the cell line expressing the lower level of N-cad, here labeled red, envelops the cell line expressing higher amounts of N-cad, here labeled green. Reproduced from (Foty and Steinberg, 2005).

4.2 Perspectives for future work

This work may be expanded in several ways. First, for simplicity I considered the social strategy to be binary in the explicit spatial model of chapter 3, i.e. either asocial (entailing an interaction coefficient β_{AA}) or social (entailing a cost c and an interaction force $\beta_{SS} > \beta_{AA}$). However, one can consider that sociality depends, for instance, on the secretion of an adhesive polymer in a variable quantity, that is encoded in the adhesion gene. This would change the trait under selection from a binary trait to a continuous trait, associated with a cost that is a growing function of the entailed adhesiveness $c = c(\beta)$. Such change in the model might lead to richer evolutionary dynamics, as from some point a costly increase in adhesiveness is of no use for individuals. Evolution might then lead to a monomorphic population endowed with a unique (optimal) adhesion coefficient β or, more intricately, a polymorphism of adhesion traits whose distribution is not straightforward. As specific ranges for microscopic parameters are required for a social mutation to be selected, and as these ranges may change as a function of the different interaction force intensities at play in the population, it is not said that successive pro-social mutations will invade for any set of microscopic and ecological parameters. The outcome is thus tricky to conjecture, and extensive computations will be needed.

A second aspect to investigate is to let parameters other than the adhesion intensity evolve; indeed, there are other ways to enhance the amount of interactions such as a larger interaction radius, that can themselves relate to “being social”. We showed for instance that too high a velocity puts the population to a gas state, while too low a velocity impedes assortment, and both these features of the population structure are detrimental to sociality. Exploring how adhesion forces co-evolve with velocity may account for social specializations relevant in the microbial world: superadhesive individuals, explorators, long-distance attractors, etc. (Guttal and Couzin, 2010)

Lastly, we opted for very basic rules of interaction as a blueprint to study collective motion and social evolution jointly. In a second step, these rules could be enriched to fit a specific microorganism, implementing additional components in the SPP model such as alignment terms, chemotaxic processes, etc.

Bibliography

André, J.B., and Baumard, N. 2011. The evolution of fairness in a biological market. Evolution 65, 1447-1456. ► **106**

Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P.D., and Nowak, M.A. 2009. Evolution of cooperation by phenotypic similarity. Proc. Natl. Acad. Sci. USA 106, 8597-8600. ► **147**

Archetti, M., and Scheuring, I. 2010. Coexistence of cooperation and defection in public goods games. Evolution. 65, 1140-1148. ► **20, 41, 93, 94**

Archetti, M., and Scheuring, I. 2012. Review: Game theory of public goods in one-shot social dilemmas without assortment. J. Theor. Biol. 299, 9-20. ► **20, 22, 24**

Avilés, L., 2002. Solving the freeloaders paradox: genetic associations and frequency dependent selection in the evolution of cooperation among relatives. Proc. Natl. Acad. Sci. USA 99, 14268-14273. ► **7, 29, 36, 40, 81, 121**

Axelrod, R., and Hamilton, W.D. 1981. The evolution of cooperation. Science 211, 1390-1396. ► **36**

Axelrod, R. 1984. *The evolution of cooperation*. Basic Books. ► **9, 106**

Bachmann, H., Molenaar, D., Kleerebezem, M., and Vlieg, J.E.T.V. 2011. High local substrate availability stabilizes a cooperative trait. ISME J. 5, 929-932. ► **14**

Bai, L., Eyiyurekli, M., Lelkes, P.I., and Breen, D.E. 2013. Self-organized sorting of heterotypic agents via a chemotaxis paradigm. Sci. Comput. Program. 78, 594-611. ► **92**

Barabási, A.-L., and Albert, R. Emergence of scaling in random networks. Science 286, 509-512. ► **25**

Beatrici, C.P., and Brunnet, L.G. 2011. Cell sorting based on motility differences. Phys. Rev. E 84, 031927. ► **84, 92**

Belmonte, J.M., Thomas, G.L., Brunnet, L.G., de Almeida, R.M.C., and Chaté, H. 2008. Self-propelled particle model for cell-sorting phenomena. Phys. Rev. Lett. 100, 248702. ► **84, 92**

Bonabeau, E., Dagorn, L., and Fron, P. 1999. Scaling in animal group-size distributions. Proc. Natl. Acad. Sci. USA 96, 4472-4477. ▶ **77**

Borenstein, D.B., Meir, Y., Shaevitz, J.W., and Wingreen, N.S. 2013. Non-local interaction via diffusible resource prevents coexistence of cooperators and cheaters in a lattice model. PLoS One 8, e63304. ▶ **31, 93**

Boyd, R., Gintis, H., Bowles, S., and Richerson, P.J. 2003. The evolution of altruistic punishment. Proc. Natl. Acad. Sci. USA 100, 3531-3535. ▶ **10**

Brown, S.P., and Buckling, A. 2008. A social life for discerning microbes. Cell 135, 600-603. ▶ **12**

Buckling, A., Maclean, R.C., Brockhurst, M.A., and Colegrave, N. 2009. The Beagle in a bottle. Nature 457, 824-829. ▶ **4**

Calovi, D.S., Brunnet, L.G., and de Almeida, R.M. 2010. cAMP diffusion in Dictyostelium discoideum: a Green's function method. Phys. Rev. E 89, 011909. ▶ **108, 126**

Cardillo, A., Meloni, S., Gómez-Gardeñes, J., and Moreno, Y. 2012. Velocity-enhanced cooperation of moving agents playing public goods games. Phys. Rev. E 85, 067101. ▶ **28, 100, 106**

Celiker, H., and Gore, J. 2013. Cellular cooperation: insights from microbes. Trends Cell. Biol. 23, 9-14. ▶ **5, 80**

Chen, Z., Gao, J., Cai, Y., and Xu, X. 2011a. Evolutionary prisoner's dilemma game in flocks. Physica A 390, 50-56. ▶ **28, 77, 81**

Chen, Z., Gao, J., Cai, Y., and Xu, X. 2011b. Evolution of cooperation among mobile agents. Physica A 390, 1615-1622. ▶ **28, 77, 81**

Chuang, J.S., Rivoire, O., and Leibler, S. 2009. Simpson's paradox in a synthetic microbial system. Science 323, 272-275. ▶ **29, 36, 71, 72**

Clutton-Brock, T.H., and Parker, G.A. 1995. Punishment in animal societies. Nature 373, 209-216. ▶ **10**

Coates, J.C., and Harwood, A.J. 2001. Cell-cell adhesion and signal transduction during Dictyostelium development. J. Cell Sci. 114, 4349-4358. ▶ **83**

Codling, E.A., Plank, M.J., and Benhamou, S. 2008. Random walk models in biology. J. R. Soc. Interface 5, 813-834. ▶ **83**

Cornforth, D.M., Sumpter, D.J.T., Brown, S.P., and Brännström, Å. 2012. Synergy and group size in microbial cooperation. Am. Nat. 180, 296-305. ▶ **20, 41**

Cremer, J., Melbinger, A., and Frey, E. 2012. Growth dynamics and the evolution of cooperation in microbial populations. Sci. Rep. 2, 281. ▶ **29, 90, 113, 115, 116**

Crespi, B.J. 2001. The evolution of social behavior in microorganisms. Trends Ecol. Evol. 16, 178-183. ▶ **5, 38, 80**

Darwin, C. 1871. *The descent of man, and selection in relation to sex.* ▶ **2**

Dawkins, R. 1976. *The selfish gene*. Oxford Univ. Press. ▶ **12, 38, 74, 106, 120**

Doebeli, M., Hauert, C., and Killingback, T. 2004. The evolutionary origin of cooperators and defectors. Science 306, 859-862. ▶ **61**

Doebeli, M., and Hauert, C. 2005. Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. Ecol. Lett. 8, 748-766. ▶ **26, 36**

Driscoll, W.W., and Pepper, J.W. 2010. Theory for the evolution of diffusible external goods. Evolution 64, 2682-2687. ▶ **31, 93**

Dubravcic, D., van Baalen, M., and Nizak, C., submitted. Bet hedging between unicellular and multicellular responses to starvation stress in Dictyostelium social amoebae. ▶ **48, 92, 106, 108, 127**

Dunbar, R.I.M. 1993. Coevolution of neocortical size, group size and language in humans. Behav. Brain Sci. 16, 681-735. ▶ **73**

Eshel, I., and Cavalli-Sforza, L.L. 1982. Assortment of encounters and evolution of cooperativeness. Proc. Natl. Acad. Sci. USA 79, 1331-1335. ▶ **74, 147**

Fehr, E., and Gächter, S. 2002. Altruistic punishment in humans. Nature 415, 137-140. ▶ **10**

Flack, J.C., Girvan, M., de Waal, F.B.M., and Krakauer, D.C. 2006. Policing stabilizes construction of social niches in primates. Nature 439, 426-429. ▶ **10**

Fletcher, J.A., and Zwick, M. 2004. Strong altruism can evolve in randomly formed groups. J. Theor. Biol. 228, 303-313. ▶ **29, 39, 90, 116, 121**

Fletcher, J.A., and Zwick, M. 2006. Unifying the theories of inclusive fitness and reciprocal altruism. Am. Nat. 168, 252-262. ▶ **105**

Fletcher, J.A., and Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. Proc. R. Soc. B 276, 13-19. ▶ **12, 19, 38, 41, 43, 105**

Foty, R.A., and Steinberg, M.S. 2005. The differential adhesion hypothesis: a direct evaluation. Dev. Biol. 278, 255-273. ▶ **126, 127, 128**

Garcia, T., and De Monte, S. 2013. Group formation and the evolution of sociality. Evolution, 67, 131-141. ▶ **81, 85, 88, 96, 106**

Gardner, A., and West, S.A. 2010. Greenbeards. Evolution 45, 25-38. ▶ **38, 74, 147**

Gardner, A., West, S.A., and Wild, G. 2011. The genetical theory of kin selection. J. Evol. Biol. 24, 1020-1043. ▶ **11**

Geritz, S.A.H., Kisdi, É., Meszéna, G., and Metz, J.A.J. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12, 35-57. ▶ **61, 62, 64**

Gibbs, K.A., Urbanowski, M.L., and Greenberg, E.P. 2008. Genetic determinants of self identity and social recognition in bacteria. Science 321, 256-259. ▶ **13, 120**

Glazier, J.A., and Graner, F. 1993. Simulation of the differential adhesion driven rearrangement of biological cells. Phys. Rev. E 47, 2128-2154. ▶ **92**

Godfrey-Smith, P. 2008. *Darwinian populations and natural selection*. Oxford Univ Press. ▶ **82**

Godfrey-Smith, P., and Kerr, B. 2009. Selection in ephemeral networks. Am. Nat. 174, 906-911. ▶ **82**

Golé, L., Rivière, C., Hayakawa, Y., Rieu, J.-P. 2011. A quorum-sensing factor in vegetative Dictyostelium Discoideum cells revealed by quantitative migration analysis. PLoS One, 6, e26901. ▶ **83, 107**

Gore, J., Youk, H., and van Oudenaarden, A. 2009. Snowdrift game dynamics and facultative cheating in yeast. Nature 459, 253-256. ▶ **7, 14, 22, 23**

Graner, F., and Glazier, J.A. 1992. Simulation of biological cell sorting using a 2-dimensional extended Potts-model. Phys. Rev. Lett. 69, 2013-2016. ▶ **92**

Greig, D., and Travisano, M. 2004. The Prisoner's Dilemma and polymorphism in yeast SUC genes. Proc. R. Soc. Lond. B 271, S25-26. ▶ **25**

Grégoire, G., Chaté, H., Tu, Y.H. 2003. Moving and staying together without a leader. Physica D 181, 157-170. ▶ **83, 91**

Grégoire, G., Chaté, H. 2004. Onset of collective and cohesive motion. Phys. Rev. Lett. 92, 025702. ▶ **83, 84, 91, 108**

Griffin, A.S., West, S.A., and Buckling, A. 2004. Cooperation and competition in pathogenic bacteria. Nature 430, 1024-1027. ▶ **6**

Guttal, V., and Couzin, I.D. 2010. Social interactions, information use, and the evolution of collective migration. Proc. Natl. Acad. Sci. USA 107, 16172-16177. ▶ **81, 129**

Guven, C., Rericha, E., Ott, E., and Losert, W. 2013. Modeling and measuring signal relay in noisy directed migration of cell groups. PLoS Comp. Biol. 9, e1003041. ▶ **83**

Hamilton, W.D. 1964. The genetical evolution of social behaviour I & II. J. Theor. Biol. 7, 1-52. ▶ **2, 11, 36, 74**

Hardin, G. 1968. The tragedy of the commons. Science 162, 1243-1248. ▶ **7, 36**

Hauert, C., De Monte, S., Hofbauer, J., and Sigmund, K. 2002. Replicator dynamics for optional public good games. J. Theor. Biol. 218, 187-194. ▶ **20, 29, 36, 81, 106, 121**

Hauert, C., De Monte, S., Hofbauer, J., and Sigmund, K. 2002. Volunteering as red queen mechanism for cooperation in public goods games. Science 296, 1129-1132. ▶ **20, 36, 81, 106, 121**

Hauert, C., Holmes, M., and Doebeli, M. 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. Proc. R. Soc. Lond. B. 273, 2565-2570. ▶ **36, 71, 81**

Hauert, C., Michor, F., Nowak, M.A., and Doebeli, M. 2006. Synergy and discounting of cooperation in social dilemmas. J. Theor. Biol. 239, 195-202. ▶ **41, 94**

Hofbauer, J., and Sigmund, K. 1998. *Evolutionary games and population dynamics*. Cambridge University Press. ▶ **44, 45, 80**

Houchmandzadeh, B. 2008. Neutral clustering in a simple experimental ecological community. Phys. Rev. Lett. 101, 078103. ▶ **108**

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215-268. ▶ **40**

Jansen, V.A.A., and van Baalen, M. 2006. Altruism through beard chromodynamics. Nature 440, 663-666. ▶ **13, 147**

Jiang, Y., Levine, H., and Glazier, J. 1998. Possible cooperation of differential adhesion and chemotaxis in mound formation of Dictyostelium. Biophys. J. 75, 2615-1625. ▶ **5, 108**

Julou, T., Mora, T., Guillon, L., Croquette, V., Schalk, I.J., Bensimon, D., and Desprat, N. 2013. Cell-cell contacts confine public goods diffusion inside Pseudomonas aeruginosa clonal microcolonies. Proc. Natl. Acad. Sci. USA 110, 12577-12582. ▶ **93**

Kappeler, P.M., and van Schaik, C.P. 2002. Evolution of primate social systems. Int. J. Primatol. 23, 707-740. ▶ **3**

Keller, L., and Ross, K.G. 1998. Selfish genes: a green beard in the red fire ant. Nature 394, 573-575. ▶ **13, 120**

Killingback, T., Bieri, J., and Flatt, T. 2006. Evolution in group-structured populations can resolve the tragedy of the commons. Proc. R. Soc. Lond. B. 273, 1477-1481. ▶ **29, 39, 116, 121**

Kollock, P. 1998. Social dilemmas: the anatomy of cooperation. Annu. Rev. Sociol. 24, 183-214. ► **36**

Koschwanez, J.H., Foster, K.R., and Murray, A.W. 2011. Sucroze utilization in budding yeast as a model for the origin of undifferentiated multicellularity. PLoS Biol. 9, e1001122. ► **82**

Kümmerli, R., Griffin, A.S., West, S.A., Buckling, A., and Harrison, F. 2009. Viscous medium promotes cooperation in the pathogenic bacterium Pseudomonas aeruginosa. Proc. R. Soc. B 276, 3531-3538. ► **82**

Kun, Á., Boza, G., and Scheuring, I. 2010. Cooperators unite! Assortative linking promotes cooperation particularly for medium sized associations. BMC Evol. Biol. 10, 173-182. ► **106**

Kutschera, U., and Niklas, K.J. 2004. The modern theory of biological evolution: an expanded synthesis. Naturwissenschaften 91, 255-276. ► **3**

Lehmann, L., and Keller, L. 2006. The evolution of cooperation and altruism – a general framework and a classification of models. J. Evol. Biol. 19, 1365-1376. ► **9**

Leimar, O., and Hammerstein, P. 2006. Facing the facts. J. Evol. Biol. 19, 1403-1405. ► **26**

Li, L., Cox, E.C., and Flyvbjerg, H. 2011. "Dicty dynamics": Dictyostelium motility as persistent random motion. Phys. Biol. 8, 046006. ► **83**

Li, S.I., and Purugganan, M.D. 2011. The cooperative amoeba: Dictyostelium as a model for social evolution. Trends Genet. 27(2), 48-53. ► **5**

MacLean, R.C., Fuentes-Hernandez, A., Greig, D., Hurst, L.D., and Gudelj, I. 2010. A mixture of "cheats" and "co-operators" can enable maximal group benefit. PLoS Biol. 8, e1000486. ► **24**

Matessi, C., and Jayakar, S.D., 1976. Conditions for the evolution of altruism under Darwinian selection. Th. Pop. Biol. 9, 360-387. ► **71, 147**

Maynard-Smith, J., and Price, G.R. 1973. The logic of animal conflict. Nature 246, 15-18. ► **3**

Maynard-Smith, J. 1982. *Evolution and the theory of games*. Cambridge Univ. Press. ► **3**

Maynard-Smith, J., and Szathmáry, E. 1995. *The major transitions in evolution*. Oxford Univ. Press. ► **2**

McNamara, J.M., Barta, Z., Fromhage, L., and Houston, A.I. 2008. The coevolution of choosiness and cooperation. Nature 451, 189-192. ► **106**

Melis, A.P., and Semmann, D. 2010. How is human cooperation different? Phil. Trans. R. Soc. B 365, 2663-2674. ► **3**

Meloni, S., Buscarino, A., Fortuna, L., Frasca, M., Gómez-Gardeñes, J., et al. 2009. Effects of mobility in a population of prisoners dilemma players. Phys. Rev. E 79, 067101. ► **28, 100, 102, 106**

Michod, R.E., and Roze, D. 2001. Cooperation and conflict in the evolution of multicellularity. Heredity 86, 1-7. ► **4, 82**

Nadell, C.D., Xavier, J.B., and Foster, K.R. 2009. The sociobiology of biofilms. FEMS Microbiol. Rev. 33, 206-224. ► **6**

Nadell, C.D., Foster, K.R., and Xavier, J.B. 2010. Emergence of spatial structure in cell groups and the evolution of cooperation. PLoS Comp. Biol., 6, e1000716. ► **81, 82, 109**

Nanjundiah V., and Sathe S. 2011. Social selection and the evolution of cooperative groups: the example of the cellular slime moulds. Integr. Biol. 3, 329-342. ► **5, 38**

Nedelcu, A., Driscoll, W.W., Durand, P.M., Herron, M.D., and Rashidi, A. 2011. On the paradigm of altruistic suicide in the unicellular world. Evolution 65, 3-20. ► **6**

Nowak, M.A., and May, R.M. 1992. Evolutionary games and spatial chaos. Nature 359, 826-828. ► **25, 26, 36**

Nowak, M.A., and Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. Nature 393, 573-577. ► **9, 36, 106**

Nowak, M.A. 2006. Five rules for the evolution of cooperation. Science 314, 1560-1563. ► **9**

Nowak, M.A., Tarnita, C.E., and Wilson, E.O. 2010. The evolution of eusociality. Nature 466, 1057-1062. ► **3, 11, 121**

Nowak, M.A., Tarnita, C.E., and Antal, T. 2010. Evolutionary dynamics in structured populations. Phil. Trans. R. Soc. B 365, 19-30. ► **25**

Okubo, A. 1986. Dynamical aspects of animal grouping: swarms, schools, flocks and herds. Adv. Biophys. 22, 1-94. ► **77**

Olson, M. 1971. *The logic of collective action*. Harvard Univ. Press, pp. 16-65. ► **37, 51, 80**

Pacheco, J.M., Traulsen, A., and Nowak, M.A. 2006. Active linking in evolutionary games. J. Theor. Biol. 243, 437-443. ► **28, 81**

Palsson, E., and Othmer, H.G. 2000. A model for individual and collective cell movement in Dictyostelium discoideum. Proc. Natl. Acad. Sci. USA 97, 10448-10453. ► **126**

Peña, J. 2012. Group size diversity in public goods games. Evolution. 66, 623-636. ► **29, 36**

Pepper, J.W. 2000. Relatedness in trait group models of social evolution. J. Theor. Biol. 224, 115-126. ► **53**

Perc, M., and Szolnoki, A. 2010. Coevolutionary games – a mini review. Biosystems 99, 109-125. ▶ **27**

Perc, M., Gómez-Gardeñes, J., Szolnoki, A., Floría, L.M., and Moreno, Y. 2013. Evolutionary dynamics of group interactions on structured populations: a review. J. R. Soc. Interface 10, 20120997. ▶ **18, 26, 27, 81**

Peruani, F., Starruß, J., Jakovljevic, V., Søgaard-Andersen, L., Deutsch, A., and Bär, M. 2012. Collective motion and nonequilibrium cluster formation in colonies of gliding bacteria. Phys. Rev. Lett. 108, 098102. ▶ **83, 108**

Pfeiffer, T., and Bonhoeffer, S. 2003. An evolutionary scenario for the transition to undifferentiated multicellularity. Proc. Natl. Acad. Sci. USA 100, 1095-1098. ▶ **36, 81**

Pfeiffer, T., Rutte, C., Killinback, T., Taborsky, M. and Bonhoeffer, S. 2005. Evolution of cooperation by generalized reciprocity. Proc. R. Soc. B 272, 1115-1120. ▶ **10, 106**

Pinker, S., and Bloom, P. 1990. Natural language and natural selection. Behav. Brain Sci. 13, 707-784. ▶ **74**

Pinheiro, F.L., Pacheco, J.M., and Santos, F.C. 2012. From local to global dilemmas in social networks. PLoS One 7, e32114. ▶ **27**

Ponte, E., Bracco, E., Faix, J., and Bozzaro, S. 1998. Detection of subtle phenotypes: The case of the cell adhesion molecule csA in Dictyostelium. Proc. Natl. Acad. Sci. USA 95, 9360-9365. ▶ **5, 13, 73, 88, 120**

Powers, S.T., Penn, A.S., and Watson, R.A. 2011. The concurrent evolution of cooperation and the population structures that support it. Evolution 65, 1527-1543. ▶ **29, 37, 71, 81, 106, 121, 124**

Queller, D.C., Ponte, E., Bozzaro, S., and Strassmann, J.E. 2003. Single-gene greenbeard effects in the social amoeba Dictyostelium discoideum. Science 299, 105-106. ▶ **13**

Rainey, P.B., and Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. Nature 394, 69-72. ▶ **98**

Rainey, P.B., and Rainey, K. 2003. Evolution of cooperation and conflict in experimental bacterial populations. Nature 425, 72-74. ▶ **6, 7**

Rainey, P.B. 2007. Unity from conflict. Nature 446, 616-616. ▶ **6**

Rainey, P.B., and Kerr, B. 2010. Cheats as first propagules: a new hypothesis for the evolution of individuality during the transition from single cells to multicellularity. Bioessays 32, 872-880. ▶ **4**

Rankin, D.J., Bargum, K., and Kokko, H. 2007. The tragedy of the commons in evolutionary biology. Trends Ecol. Evol. 22, 643-651. ▶ **7, 36**

Ratcliff, W.C., Denison, R.F., Borrello, M., and Travisano, M. 2012. Experimental evolution of multicellulariy. Proc. Natl. Acad. Sci. USA 109, 1595-1600. ▶ **4, 6**

Ratnieks, F.L.W., Foster, K.R., and Wenseleers, T. 2006. Conflict resolution in insect societies. Annu. Rev. Entomol. 51, 581-608. ▶ **3**

Reiczigel, J., Lang, Z., Rózsa, L., and Tóthmérész, B. 2008. Measures of sociality: two different views of group size. Anim. Behav. 75, 715-721. ▶ **40**

Roca, C.P., Cuesta, J.A., Sánchez, A. 2009. Evolutionary game theory: temporal and spatial effects beyond replicator dynamics. Phys. Life Rev. 6, 208-249. ▶ **27**

Roca, C.P., and Helbing, D. 2011. Emergence of social cohesion in a model society of greedy, mobile individuals. Proc. Natl. Acad. Sci. USA 108, 11370-11374. ▶ **26**

Roisin-Bouffay, C., Jang, W., Caprette, D.R., and Gomer, R.H. 2000. A precise group size in Dictyostelium is generated by a cell-counting factor modulating cell-cell adhesion. Mol. Cell 6, 953-959. ▶ **107**

Riley, M.A., and Wertz, J.E. 2002. Bacteriocins: evolution, ecology and application. Ann. Rev. Microbiol. 56, 117-137. ▶ **13, 120**

Sachs, J.L. 2008. Resolving the first steps to multicellularity. Trends Ecol. Evol. 23, 245-248. ▶ **4, 82**

Sanchez, A., and Gore, J. 2013. Feedback between population and evolutionary dynamics determines the fate of social microbial populations. PLoS Biol. 11, e1001547. ▶ **109**

Santos, F.C., Pacheco, J.M., and Lenaerts, T. 2006. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. Proc. Natl. Acad. Sci. USA 103, 34903494. ▶ **27**

Santos, F.C., Santos, M.D., and Pacheco, J.M. 2008. Social diversity promotes the emergence of cooperation in public goods games. Nature 454, 213-217. ▶ **27**

Sasaki, T., and Uchida, S. 2013. The evolution of cooperation by social exclusion. Proc. R. Soc. B 280, 20122498. ▶ **106**

Schtickzelle, N., Fjerdingstad, E.J., Chaine, A., and Clobert, J. 2009. Cooperative social clusters are not destroyed by dispersal in a ciliate. BMC Evo. Biol. 9, 251. ▶ **79**

Schuster, P., and Sigmund, K. 1983. Replicator dynamics. J. Theor. Biol. 100, 533-538. ▶ **44**

Shimkets, L.J. 1986a. Correlation of energy-dependent cell cohesion with social motility in Myxococcus xanthus. J. Bacteriol. 166, 837-841. ▶ **5, 73**

Shimkets, L.J. 1986b. Role of cell cohesion in Myxococcus xanthus fruiting body formation. J. Bacteriol. 166, 842-848. ▶ **73**

Sigmund, K. 2007. Punish or perish? Retaliation and collaboration among humans. Trends Ecol. Evol. 22, 593-600. ▶ **10**

Simon, B., Fletcher, J.A., and Doebeli, M. 2012. Towards a general theory of group selection. Evolution 67, 1561-1572. ▶ **89, 109, 117**

Smukalla, S., Caldara, M., Pochet, N., Beauvais, A., Guadagnini, S., Yan, C., Vinces, M.D., Jansen, A., Prevost, M.C., Latgé, J.P., Fink, G.R., Foster, K.R., Verstrepen, K.J. 2008. FLO1 is a variable green beard gene that drives biofilm-like cooperation in budding yeast. Cell 135, 726-737. ▶ **5, 13, 38, 48, 52, 61, 88, 92, 106, 120, 124, 126, 128**

Strassmann, J.E., and Queller, D.C. 2011. Evolution of cooperation and control of cheating in a social microbe. Proc. Natl. Acad. Sci. USA 108, 10855-10862. ▶ **5, 47, 73, 83**

Strassmann, J.E., Gilbert, O.M., and Queller, D.C. 2011. Kin discrimination and cooperation in microbes. Annu. Rev. Microbiol. 65, 349-367. ▶ **106**

Sumpter, D.J.T., 2010. *Collective animal behavior.* Princeton Univ. Press. ▶ **2, 25**

Szathmáry, E. 2011. To group or not to group? Science 334, 1648-1649. ▶ **6**

Szolnoki, A., and Perc, M. 2012. Conditional strategies and the evolution of cooperation in spatial public goods games. Phys. Rev. E 85, 026104. ▶ **10**

Tang, L., Gao, T., McCollum, C., Jang, W., Vicker, M.G., Ammann, R.R., and Gomer, R.H. 2002. A cell number-counting factor regulates the cytoskeleton and cell motility in Dictyostelium. Proc. Natl. Acad. Sci. USA 99, 1371-1376. ▶ **52, 124**

Tarnita, C.E., Antal, T., Ohtsuki, H., and Nowak, M.A. 2009. Evolutionary dynamics in set structured populations. Proc. Natl. Acad. Sci. USA 106, 8601-8604. ▶ **30**

Taylor, P.D., and Jonker, L.B. 1978. Evolutionary stable strategies and game dynamics. Math. Biosci. 40, 145-156. ▶ **44, 45**

Taylor, C., and Nowak, M.A. 2006. Evolutionary game dynamics with non-uniform interaction rates. Theor. Pop. Biol. 69, 243-252. ▶ **48, 85**

Traulsen, A., and Nowak, M.A. 2006. Evolution of cooperation by multilevel selection. Proc. Natl. Acad. Sci. USA 103, 10952-10955. ▶ **29, 39, 116, 121**

Trivers, R.L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35-57. ▶ **36, 106**

Vainstein, M.H., Silva, A.T.C., Arenzon, J.J. 2007. Does mobility decrease cooperation? J. Theor. Biol. 244, 722-728. ▶ **26**

Van Dyken, J.D., Müller, M.J.I., Mack, K.M.L., and Desai, M.M. 2013. Spatial population expansion promotes the evolution of cooperation in an experimental prisoner's dilemma. Curr. Biol. 23, 919-923. ▶ **82** van Oss, C., Panfilov, A.V., Hogeweg, P., Siegert, F., and Weijer, C.J. 1996. Spatial pattern formation during aggregation of the slime mould Dictyostelium discoideum. J. Theor. Biol. 181, 203-213. ► **126**

van Veelen, M., García, J., and Avilés, A. 2010. It takes grouping and cooperation to get sociality. J. Theor. Biol. 264, 1240-1253. ► **29, 36, 81**

Velicer, G.J. 2003. Social strife in the microbial world. Trends Microbiol. 11, 330-337. ► **5, 73, 79, 80**

Velicer, G.J., and Yu, Y.N. 2003. Evolution of novel cooperative swarming in the bacterium Myxococcus xanthus. Nature 425, 75-78. ► **5, 73, 88**

Vicsek, T., Czirók, A., Ben-Jacob, E., Cohen, I., and Shochet, O. 1995. Novel type of phase transition in a system of self-driven particles. Phys. Rev. Lett. 1995, 1226-1229. ► **77, 83, 91, 108**

Villone, D., Robledo, A., and Sánchez, A. 2011. Chaos and unpredictability in evolutionary dynamics in discrete time. Phys. Rev. Lett. 107, 038101. ► **44, 45**

Watts, D.J., and Strogatz, S.H. 1998. Collective dynamics of "small world" networks. Nature 393, 440-442. ► **25**

Waxman, D., and Gavrilets, S. 2005. 20 questions on adaptive dynamics. J. Evol. Biol. 18, 1139-1154. ► **61, 62**

Wedekind, C., and Milinski, M. 2000. Cooperation through image scoring in humans. Science 288, 850-852. ► **106**

West, S.A., Griffin, A.S., Gardner, A., and Diggle, S.P. 2006. Social evolution theory for microorganisms. Nat. Rev. Microbiol. 4, 597-607. ► **38**

West, S.A., Diggle, S.P., Buckling, A., Gardner, A., and Griffin, A.S. 2007a. The social lives of microbes. Annu. Rev. Ecol. Evol. Syst. 38, 53-77. ► **5, 80**

West, S.A., Griffin, A.S., and Gardner, A. 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415-432. ► **9, 74**

West, S.A., and Gardner, A. 2010. Altruism, spite and greenbeards. Science 327, 1341-1344. ► **147**

Wilson, D.S. 1975. A theory of group selection. Proc. Natl. Acad. Sci. USA 72, 143-146. ► **29, 36**

Wilson, D.S. 1979. Structured demes and trait-group variation. Am. Nat. 113, 606-610. ► **53**

Wilson, S.D., and Dugatkin, L.A., 1997. Group selection and assortative interactions. Am. Nat. 149, 336-351. ► **12, 29, 40, 105, 147**

Wolpert, L., and Szathmáry, E. 2002. Multicellularity: evolution and the egg. Nature 420, 745-745. ► **4**

Xavier, J. 2011. Social interactions in synthetic and natural microbial communities. Mol. Syst. Biol. 7, 483. ► **79**

Zhang, J., Wang, W., Du, W., and Cao, X. 2011a. Evolution of cooperation among mobile agents with heterogenous view radii. Physica A 390(12), 2251-2257. ► **81**

Zhang, Y., Thomas, G.L., Swat, M., Shirinifard, A., and Glazier, J.A. 2011b. Computer simulations of cell sorting due to differential adhesion. PLoS One 6, e24999. ► **84, 92**

Appendix A

Derivation of the payoff difference, general case

In the manuscript, I have derived the condition for the evolution of sociality in the case of groups formed by serial adhesion events, each independent of the group composition. This implies that there is no assortment within groups. Here, I discuss the general formulation of the payoff difference between **S** and A individuals when both differential group size repartition and within-group assortment come into play. This typically occurs when other than unconditional differences in adhesion probability, recognition mechanisms or signals can influence the process of group formation.

Let us remind the payoff received by a social individual in a group of size $n > 1$ where m of the $n - 1$ co-players are social:

$$P_s(m, n) = b\,\frac{m+1}{n} - c$$

and that of an asocial individual:

$$P_a(m, n) = b\,\frac{m}{n}$$

Individuals form groups according to some rules for aggregation. Let x denote the frequency of social individuals. To lighten notations, I will thereafter assume all probabilities to be conditional to the aggregation rules and x.

The computation of the payoff is performed in two steps, related to the demic structure of the social game. First, one finds the payoff difference within a group of given size, thus accounting for differential assortment between types. Second, the average payoff difference of the two strategies is computed weighting within-group payoffs according to the size distribution, thus reflecting the allocation of individuals of the two types to groups of different sizes.

The average payoff difference between *S* and **A** players in a population with group size heterogeneity is:

$$\Delta P = \sum_{n\geq 1} \left[d_S(n)\, P_s(n) \; - \; d_a(n)\, P_a(n) \right] \tag{A.1}$$

where:

$$P_s(n) = \sum_{m=0}^{n-1} b\, \frac{m+1}{n}\, p_s(m|n) - \; c \tag{A.2}$$

and

$$P_a(n) = \sum_{m=0}^{n-1} b\, \frac{m}{n}\, p_a(m|n). \tag{A.3}$$

are the expected payoffs received by *S*s and *A*s, given the group has size n ($n \geq 2$) and it contains m social coplayers. The probabilities $p_s(m|n)$ and $p_a(m|n)$ that a *S* (resp. *A*) individual encounters m *S*s among its $n-1$ associates characterize the assortment resulting from the aggregation process.

By substitution of eqs. (A.2) and (A.3) into eq. (A.1), we obtain the following general expression for the payoff difference between social and asocial players:

$$\Delta P = b \sum_{n\geq 2} \frac{1}{n} \left[d_s \sum_{m=0}^{n-1} m\, p_s(m|n) - d_a \sum_{m=0}^{n-1} m\, p_a(m|n) + d_s \right] - c. \tag{A.4}$$

The benefit term in this equation depends on the balance between the average sociality levels in groups experienced by a *S* (resp. *A*) player, weighted by the relative abundance of these groups.

In order to pinpoint the relative role of assortment and group size heterogeneity, I now explicitly compute this payoff difference for three extreme cases: 1) groups all have the same size; 1) *S* and *A* players segregate; in 3), I recover the case described in the manuscript when group size is distributed and within-group assortment is random. The first two examples are instances of the case when within-group assortment is made positive by recognition mechanisms amongst players.

Groups of identical size In the particular case of fixed group size n^*, the payoff difference writes

$$\Delta P(n^*) = \frac{b}{n^*} \left[\sum_{m=0}^{n^*-1} m\left(p_s(m) - p_a(m)\right) + 1 \right] - c \tag{A.5}$$

If there is no positive assortment within the social type, the condition for sociality to evolve reduces to $b/c > n^*$, which is stringent in particular if n^* is large. Assortative group formation, however, can lead to a positive payoff difference even for smaller benefit to cost ratios. Since the probabilities $p_s(m)$ and $p_a(m)$ both sum up to 1, then if $p_s(m) > p_a(m)$ for large m (that is, if social individuals tend to aggregate more with individuals of their type) the quantity $m\left(p_s(m) - p_a(m)\right)$ is positive and can compensate the cost. Positive assortment has long been reported as a way to ensure the evolution of cooperative behavior, and has spawned numerous theoretical studies in the case of fixed group size (see for instance Antal et al. (2009); Eshel and Cavalli-Sforza (1982); Matessi and Jayakar (1976); Wilson and Dugatkin (1997)).

Perfect segregation An extreme case of group formation is perfect group segregation (through, for instance, green beard mechanisms; see Jansen and van Baalen (2006); West and Gardner (2010); Gardner and West (2010)). In this case, assortment is total, i.e. $p_s(n-1|n) = 1$, thus

$p_s(m \neq n-1|n) = 0$; $p_a(0|n) = 1$, thus $p_a(m \neq 0|n) = 0$. As a consequence, $P_s(n) = b - c$ and $P_a(n) = 0$ when $n \geq 2$ so that

$$\Delta P = b\,(1 - l_s)\; - \; c \tag{A.6}$$

where $l_s = d_s(1)$ is the proportion of social individuals left alone (therefore $1 - ls$ that of social individuals that are in a group). Here ΔP does not depend on how group size is distributed. In this favorable setting, sociality may evolve easily as soon as the proportion of lonely *S*s is small. In the limit case when all socials enter one group, that is $l_s = 0$, sociality evolves under the weakest possible condition $b/c > 1$.

Heterogeneous group size, no within-group assortment Even in the absence of within-group assortment ($p_s = p_a$), sociality can evolve if *S*s and *A*s players are unevenly distributed between groups, so that sociality corresponds to higher expectations for the size of the group one belongs to.

This is the case we discuss in the manuscript, where groups are formed via sequential pairwise interaction of individuals possensing different attachment probability. Under such group formation process, no within-group assortment emerges:

$$p_s(m|n) = p_a(m|n) = \binom{n-1}{m}\, p_s(n)^m\, p_a(n)^{n-1-m}\; \forall m, n \tag{A.7}$$

The number of social co-members expected, given a size n, is thus the same:

$$\sum_{n=0}^{n-1} m\, p_s(m|n) = \sum_{n=0}^{n-1} m\, p_a(m|n) := \bar{m} \tag{A.8}$$

with

$$\bar{m} = (n-1)\, p_s(n) = (n-1)\, \frac{x\, d_s(n)}{x\, d_s(n) + (1-x)\, d_a(n)} \tag{A.9}$$

The hypothesis of non-assortative aggregation made in the manuscript is conservative: if positive assortment is further assumed, sociality evolves even more easily. Indeed, under positive within group assortment $\sum m\, p_s(m|n) > \bar{m}$ (and correspondingly, $\sum m\, p_a(m[n) < \bar{m}$), so that the payoff difference in eq. (A.4) increases.

Appendix B

Group size distributions for differential attachment

Let us first consider social players. We distinguish two cases: 1) the focal social player is a recruiter (with probability $1/T$); 2) the focal social player is not a recruiter (with probability $(1-1/T)$). In what follows, we denote $Q_s(x) = x\pi_{ss}+(1-x)\pi_{as}$ and $Q_a(x) = x\pi_{as}+(1-x)\pi_{aa}$ the probabilities that a random player attaches to a social (resp. asocial) recruiter.

Case 1: The focal social player is a recruiter: Its group has size n whenever $n-1$ individuals among the $T-1$ in its set attach to it, i.e. with a probability

$$R_s(n,x) = \binom{T-1}{n-1} Q_s(x)^{n-1}(1-Q_s(x))^{T-n}$$

Case 2: The focal social player is not a recruiter: One has to consider whether its recruiter is social (with probability x) or asocial (with probability $(1-x)$). The probability to end up in a group of size n if the recruiter is social is:

$$r_{s,s}(n,x) = \begin{cases} 1-\pi_{ss} & \text{if } n=1 \\ \pi_{ss}\dbinom{T-2}{n-2} Q_s(x)^{n-2}(1-Q_s(x))^{T-n} & \text{if } n \geq 2 \end{cases}$$

Indeed, $n \geq 2$ means that the focal player is recruited and that $n-2$ among the remaining $T-2$ other players also attach to the social recruiter; the case $n = 1$ means that the interaction with the social recruiter does not succeed. If the focal player's recruiter is asocial, one has similarly:

$$r_{s,a}(n,x) = \begin{cases} 1-\pi_{as} & \text{if } n=1 \\ \pi_{as}\dbinom{T-2}{n-2} Q_a(x)^{n-2}(1-Q_a(x))^{T-n} & \text{if } n \geq 2 \end{cases}$$

The group size distribution for social players $d_s(n,x)$ is a linear combination of the three probability distributions $R_s(n,x)$, $r_{s,s}(n,x)$ and $r_{s,a}(n,x)$, weighted by their respective occurrence probabilities:

$$d_s(n,x) = \frac{1}{T}\,R_s(n,x) + \left(1-\frac{1}{T}\right)\,[r_{s,s}(n,x)\,x + r_{s,a}(n,x)\,(1-x)] \tag{B.1}$$

The calculation of the group size distribution for asocial players follows the same lines. In the end,

$$d_a(n,x) = \frac{1}{T}\,R_a(n,x) + \left(1-\frac{1}{T}\right)\,[r_{a,s}(n,x)\,x + r_{a,a}(n,x)\,(1-x)] \tag{B.2}$$

with

$$R_a(n,x) = \binom{T-1}{n-1} Q_a(x)^{n-1}(1-Q_a(x))^{T-n} \text{for } n \geq 1$$

$$r_{a,s}(n,x) = \begin{cases} 1-\pi_{as} & \text{if } n=1 \\ \pi_{as}\binom{T-2}{n-2} Q_s(x)^{n-2}(1-Q_s(x))^{T-n} & \text{if } n \geq 2 \end{cases}$$

$$r_{a,a}(n,x) = \begin{cases} 1-\pi_{aa} & \text{if } n=1 \\ \pi_{aa}\binom{T-2}{n-2} Q_a(x)^{n-2}(1-Q_a(x))^{T-n} & \text{if } n \geq 2 \end{cases}$$

In Fig. B.1, we represent the theoretical distributions d_a and d_s for a given set of parameters and composition x of the population.

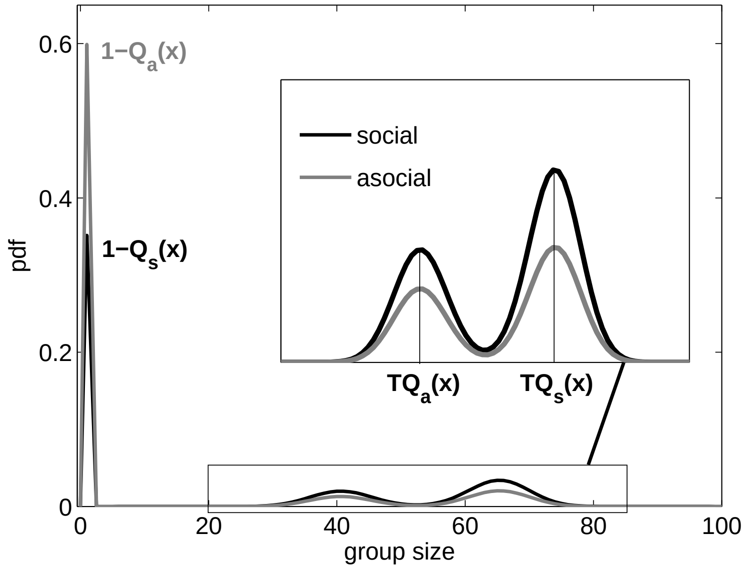

Figure B.1: Theoretical group size distributions for social and asocial individuals. Parameters values: $T = 100$, $\pi_{ss} = 0.8$, $\pi_{aa} = 0.3$, $\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}}$, $x = 0.5$.

Appendix C

Condition for sociality to be altruistic for differential attachment

The calculation of the the maximal benefit-cost-ratio $r_c(x) = \left(\sum_{n\geq 2} d_S(n)/n\right)^{-1}$ ensuring that sociality is altruistic requires the use of the following formulas:

$$\sum_{k=0}^{N} \frac{1}{k+1} \binom{N}{k} A^k\, B^{N-k} = \frac{(A+B)^{N+1} - B^{N+1}}{A(N+1)}$$
$$\sum_{k=0}^{N} \frac{1}{k+2} \binom{N}{k} A^k\, B^{N-k} = \frac{(N+2)A(A+B)^{N+1} - (A+B)^{N+2} + B^{N+2}}{A^2(N+1)(N+2)}$$

Combined with the expressions of the distribution d_S, this yields:

$$\begin{aligned} r_c(x) = \Bigg[& \frac{1}{T}\left(\frac{1-(1-Q_s)^T}{TQ_s} - (1-Q_s)^{T-1}\right) \\ & + \left(1-\frac{1}{T}\right)\left(x\,\pi_{ss}\frac{TQ_s - 1 + (1-Q_s)^T}{T(T-1)Q_s^2} + (1-x)\,\pi_{as}\frac{TQ_a - 1 + (1-Q_a)^T}{T(T-1)Q_a^2}\right)\Bigg]^{-1} \end{aligned} \tag{C.1}$$

This critical benefit-to-cost ratio, evaluated at the threshold frequency x^*, is displayed in

Fig. 3 of the main text. In the limit $T \to +\infty$,

$$r_c(x) \sim \frac{T}{x\,\pi_{ss}/Q_s + (1-x)\,\pi_{as}/Q_a} \tag{C.2}$$

and is thus linear with the maximal group size T.

Appendix D

Evolutionary algorithm for chapter 3

The following instructions are repeated at each generation $g = 1, \ldots, g_f$ until an equilibrium is reached:

Initialization

The algorithm is initialized with a population of N_{pop} particles ith positions (x, y) chosen at random on the $[0, L] \times [0, L]$ 2D square, and motion directions θ chosen at random between 0 and 2π.

Aggregation process

At each time step $t = 1, \ldots, t_f$, all particles' updated directions and positions are calculated successively according to the following steps:

1. find the focal particle's neighbors within a radius r_1;
2. calculate the interaction forces they exert on the focal particle according to Equation 1 of the main text;
3. calculate the focal particle's new direction according to Equation 2 of the main text;

4. update the focal particle's position according to Equation 3 of the main text.

Payoff allocation

Once time step $t = t_f$ is over, each particle's group (if any) is determined according to the criterion described in section 3.2.2. If the particle j's group has n_j members, among whom s_j are social, then its payoff is calculated according to a linear PGG, that is:

$$P_j = b\,\frac{s_j}{n_j} \qquad \text{if particle } j \text{ is asocial} \tag{D.1}$$

$$P_j = b\,\frac{s_j}{n_j} - c \qquad \text{if particle } j \text{ is social} \tag{D.2}$$

We assume clonal reproduction. The payoff received by each individual determines its probability to generate an offspring at the next generation. This probability is linearly determined by rescaling the payoff between two values f_{min} and f_{max} with $0 \leq fmin < fmax < 1$. The rescaling parameters allow to adjust both the speed of renewal of the population and the strength of selection.

Social frequency update

Here, we detail how the frequency $x^{(g+1)}$ of the social trait at generation $g + 1$ is determined according to its frequency $x^{(g)}$ and the average probabilities $f_s^{(g)}$ and $f_a^{(g)}$ of an S (resp. an A) particle to leave offspring at generation g.

Birth process: Let $N_s^{(g)}$ and $N_a^{(g)}$ be the number of S (resp. A) particles in the population at generation g, so that $N_s^{(g)} + N_a^{(g)} = N_{pop}$. Considering that mutations can arise at a frequency u and change the strategy of a newborn to the opposite strategy (S → A and A → S), their numbers N'_s and N'_a due to the birth process can be expressed as:

$$\begin{aligned}N'_s &= N_s^{(g)} + N_s^{(g)} f_s^{(g)}(1-u) + N_a^{(g)} f_a^{(g)} u \\ &= N_{pop}\left[x^{(g)} + x^{(g)} f_s^{(g)}(1-u) + (1-x^{(g)}) f_a^{(g)} u\right] \qquad \text{(D.3)}\end{aligned}$$

and

$$\begin{aligned}N'_a &= N_a^{(g)} + N_a^{(g)} f_a^{(g)}(1-u) + N_s^{(g)}(1+f_s^{(g)}) u \\ &= N_{pop}\left[1 - x^{(g)} + (1-x^{(g)}) f_a^{(g)}(1-u) + x^{(g)} f_s^{(g)} u\right] \qquad \text{(D.4)}\end{aligned}$$

Death process: As we want not to take into account demographic effects on the evolutionary dynamics, we maintain the population constant by means of a death process that applies indiscriminately to particles of any strategy. Each particle thus dies with a probability $d^{(g)}$ such that at generation $g+1$ the population size $N_s^{(g+1)} + N_a^{(g+1)} = N_{pop}$. Hence the survival rate $(1-d^{(g)})$ is such that $N_s^{(g+1)} = N'_s(1-d^{(g)})$ and $N_a^{(g+1)} = N'_a(1-d^{(g)})$, and combining these two conditions and Eqs. $D.3$ and $D.4$ we find:

$$1 - d^{(g)} = \frac{1}{1 + x^{(g)} f_s^{(g)} + (1-x^{(g)}) f_a^{(g)}} \qquad \text{(D.5)}$$

Thus,

$$N_s^{(g+1)} = N_{pop} \frac{x^{(g)} + x^{(g)} f_s^{(g)}(1-u) + (1-x^{(g)}) f_a^{(g)} u}{1 + x^{(g)} f_s^{(g)} + (1-x^{(g)}) f_a^{(g)}} \qquad \text{(D.6)}$$

and

$$x^{(g+1)} = N_s^{(g+1)} / N_{pop} \qquad \text{(D.7)}$$