The evolutionary iron law of oligarchy

by

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Author's declaration

This thesis is a presentation of my original research work.

Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature, and acknowledgement of collaborative research and discussions.

SIGNED: .... DATE: ....

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[1] This part is in french because my mom does not speak English and she already made several complaints about me not translating my papers and thesis for her.

Abstract

Social hierarchy is a pervasive element of modern societies, yet almost absent before the advent of agriculture during the Neolithic transition. Despite evidence supporting hierarchy as a product of evolution, it is hard to explain the mechanisms which drove this evolution. For instance, the evolution of followers appears as a paradox because followers receive fewer resources than leaders. The "iron law of oligarchy" proposes that the key to the Neolithic transition lies in the role of leaders in collective decision-making. First, leaders would emerge in response to an increase in group size because leaders speed up decision-making and facilitate coordination. Then, leaders would use their newly acquired influence to bias opinions and group decisions to impose inequality that benefits themselves. This theory has the benefit of explaining the origin of both beneficial and despotic sides of leaders. Yet, its investigation has been limited because of the lack of a formal description of (i) how individuals change with time and (ii) how individuals take collective decisions. Thus, we propose the evolutionary iron law of oligarchy, which reinterprets the iron law in evolutionary terms. We reduce leaders and followers to their capacity to influence and we claim that describing the evolution of this trait under the environmental changes observed at the Neolithic transition is sufficient to explain the emergence of helpful and despotic leaders. To investigate this claim, we build individual-centred models simulating consensus formation — how individuals take collective decisions — and evolutionary dynamics — how individuals change with time. On one hand, our results show that the evolutionary iron law of oligarchy is a viable scenario, which can unify previous theories explaining either the beneficial or despotic side of leaders. On the other hand, we developed a mechanistic model of the iron law of oligarchy which can apply across a range of scenarios, and which show under which conditions the iron law of oligarchy would apply. Finally, our results demonstrate that the iron law of oligarchy goes beyond political sciences and is underwritten by the laws of Darwinian evolution. Understanding the factors driving the emergence of hierarchy and despotism will open new perspectives to design better forms of governance.

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First Chapter

Introduction

1.1 Social hierarchy is surprisingly widespread in human societies

In 1976, the technology company Kodak created the first digital camera, a technology which would later revolutionise the camera industry. Yet, its leaders took the decision to stick with film and paper line (Lucas, 2012). At the time of the discovery, Kodak commanded over 90 % of the film market. In 2012, Kodak filed for bankruptcy. Over these three decades, the company lost roughly 80% of its workforce, over 100000 employees. This single decision had a dreadful impact on the life of numerous persons, but leaders' decisions can lead to much more sinister outcomes. In 1958, Mao Zedong leader of the People's Republic of China and the leaders of the governing political party, took the decision to reform the economic and social organisation of China (Dikotter, 2011). This campaign, called "The Great Leap Forward", included massive collectivisation and rapid industrialisation of the economy. A few years later, these policies led to an economic and social disaster; for instance the food supply dropped to 70% of the original level (Yang, 2008). Worsened by deceitful reports, this decision resulted in the Great Chinese Famine, one of the most deadly events of human history infamous for its millions of deaths.

Those are a few examples of decisions among countless ones. Who to conquer? Who to trade with? How to manage the environment? The decisions that take groups can shape their fate, and even their survival. It is then surprising that only a minority of individuals are actually involved in the decision-making process. The large majority of employees in Kodak and citizens of the Republic of China had no say on the decisions of their leaders. Whether it is in a company, kingdom or democracy, most societies have given the reins (or burden) of power to a small number of individuals. Of course, this distribution of power is often challenged as seen in recent political crises, e.g. Brexit (Clarke et al., 2017), Yellow vests movement ("Gilets jaunes: The French uprising" 2019; Vandepitte, 2019). Yet, the need for having leaders is not often questioned. Hierarchy emerges over and over despite the countless societies which have been built. In short, humans value equality but live in hierarchy. How can this paradox be explained? Ultimately, what drives the emergence and the prevalence of social hierarchy?

First, what do we exactly mean by social hierarchy and social organisation ?[1] Social organisation describes the form of distribution of power and resources within a group. Resources describes any material providing a benefit to an individual for its survival or reproduction such as money, land or mating partners. Power describes the influence that an individual has on others' behaviours and on group decisions. Social hierarchy is a particular set of instances of social organisation in which resources and power are distributed asymmetrically, i.e. concentrated in a minority of individuals. The term "social" in social hierarchy is used to differentiate it from the broader definition of hierarchy, which describes the abstract arrangement of items according to relative importance. We refer to social hierarchy as hierarchy for the rest of the thesis. The simplest form of hierarchy is described by the presence of a minority of leaders and a majority of followers. Leaders take most of the decisions and possess a large share of the resources, while followers have a limited influence on group decisions and receive a lower share of resources. Examples of leaders and followers are kings and their subjects, elected presidents and their citizens, chief executive officers (CEO) of a company and their employees. Hierarchy can describe a large range of social organisation, going from a slightly asymmetric distribution of power and resources to the most extreme form in which one individual possesses all the resources and political power, e.g. dictatorship. We use the term level of hierarchy to describe how much a group is hierarchical, that is how much power and resources are distributed asymmetrically.

The social organisation of a group is a dynamic process, which changes alongside time. Investigating the rules governing the change of social organisation can provide key knowledge to understand its benefits and costs, explain its diversity across space and time, and manage social organisation. To give an analogy, understanding the rules governing the evolution of species or the movement of planets helped us understand the biosphere and the universe. And in the same manner as the universe, human hierarchy had its big bang.

1.2 From egalitarian hunter-gatherers to hierarchical agriculturists

It is tempting to date the origin of human social hierarchy in times preceding the emergence of human species. Great apes are species closely related to modern humans (*Homo sapiens*) and they are organised in dominance hierarchies where individuals physically compete for rank, resources and partners (Sussman, 1999). Because different

[1] For now, we use a broad definition of hierarchy to encompass the literature on the subject. An exact definition of social organisation and social hierarchy for this thesis is given at section 1.7.

species of great apes share this particularity, it has been supposed that the last common ancestor of humans and apes was also organised in such hierarchy, i.e. great apes would have inherited their social organisation from this past ancestor (Chapais, 2018; Duda and Zrzavý, 2013). However, the history of human social organisation followed a surprisingly different path than that of its close cousins.

Unlike great apes, the dominance hierarchy of humans' ancestor was followed by a long period of egalitarianism (Boehm, 2001). This egalitarianism was relative in the sense that some individuals still acted as leaders in particular situations, e.g. the best hunter leads during hunts (Von Rueden et al., 2014; Garfield et al., 2019b). However, wealth was distributed relatively equally and no individual could decide by himself of the fate of other members of the group (Woodburn, 1982; Kelly, 2010; Lee and Daly, 1999; Boehm, 2001). Group decisions, e.g. start a conflict with another tribe; were taken in an egalitarian way, with every individual having the right to express their opinion. In the Australian Aborigines of Victoria, the hunter does not decide of the distribution of the game but it also often gets the worst part (Dawson, 1881). The Mbuti tribe living in the Congo bassin decides of the next group movement by a shared consensus, reached after acephaleous discussions (Turnbull, 1962). Hunter-gatherers were not all naturally inclined toward equality unlike the romantic view of hunter-gatherers developed along with the first anthropological studies (Gat, 2015) [2]. In truth, some individuals still tried to monopolise resources and powers, but their aspirations were restricted by strong egalitarian norms enforced by other members of the group (Boehm, 2001). For instance, in the tribes of hunter-gatherers observed in the last century, the distribution of food is often ruled by strict norms, which details how the food needs to be distributed (Testart, 1987). In the !Kung Bushmen, the owner of the hunted game is the owner of the first arrow to penetrate enough the skin of the animal for the poison to make effect (Marshall, 1960). Because arrows are often exchanged, the owner of the game can be someone else than the the hunter who killed it. Deviations from the egalitarian norms, e.g. not sharing food, imposing a decision; were punished by the rest of the group first by gossip, then ostracising and potentially killing. These punishments are well illustrated by the misadventures of some anthropologists. While they were studying two different tribes of hunter-gatherers, Jean Briggs and Denett Everett intervened when westerners were trying to buy goods and services from the tribes in exchange of cheap alcohol. In return, the Utku, a small group of Inuit First Nations people, casts out Jean Briggs from the village and ostracised her for months (Briggs, 1971). In the second case, the Piranã tribe threatens to kill Daniel Everett and its family. Accordingly, the hunter-gatherers' equality is sometimes described as a reverse hierarchy rather than egalitarian — a hierarchy where followers imposed dominance on the uprising leaders.

The transition from the dominance hierarchy of human ancestors to egalitarianism

[2] what Alain Testart calls "the model of the noble savage and the idea of primitive communism" (Testart, 1987).

of hunter-gatherers is the first major turning point in the history of human social organisation. Ultimately, this transition can be explained by the importance of cooperative behaviours in the new environment of humans (Gintis et al., 2015). For instance, food sharing assures a reliable source of food despite irregular hunting results. In a more proximal point of view, the development of cognitive capacities and anti-authoritarian mechanisms tilted the balance of power toward followers. For example, the capacity to form large coalitions combined with the development of throwable weapons make any dissatisfied follower a dangerous threat no matter the physical strength of the dominant individual (Bingham, 1999; Gintis et al., 2015). Thus, a strong individual could not impose anymore its dominance on the rest of the group.

Archaeological evidence, e.g. absence of difference of wealth in tombs, similar settlement size; suggests that the egalitarian organisation of human groups remained largely unmodified for hundreds of thousands of years (Boehm, 2001) [3]. It is only 12500 years ago that the first hierarchical societies emerged (Price, 1995). At this period called Neolithic transition, the advent of agriculture and the domestication of animals revolutionised the lifestyle of humans. Within a few thousand years, human societies switched from small and nomad groups of hunter-gatherers to large sedentary communities of farmers. The Neolithic transition also marks a revolution in the organisation of human societies with the emergence of chiefdoms all around the globe. Chiefdoms are political entities with a centralised decision-making, which coordinates activities among several village communities (Service, 1962; Service, 1975; Earle, 1987) [4]. The central authority of a chiefdom usually organises a regional population of thousands to ten thousands of individuals. In contrast to pre-Neolithic tribes, the leaders are permanent and can take decisions across a wide range of topics, e.g. agriculture, warfare, religion. These chiefs exhibit a higher amount of wealth. For instance, settlements and burials of leaders are larger, more central and contain more goods which can include special foreign objects achievable only by long-distance trade (see Earle 1987 or Junker 2018 for a detailed review of inequality in chiefdoms).

Later on, human social organisation continued its course toward more complex hierarchy, with in particular the emergence of bureaucratic states. States are characterised by a specialised administration dedicated to the organisation of the society

[3] There has been an ongoing debate on the archaeological evidence showing egalitarian organisation. The main criticism is that the evidence for egalitarianism is sometimes presented as an absence of evidence of hierarchy. Two main points counter this criticism. First, hierarchy and egalitarianism are mutually exclusive states of social organisation and the absence of evidence for one is thus evidence for the other. Second, it is important to not confuse absence of proof and proof of absence. For instance, evidence of egalitarianism is not shown by the absence of tombs with difference in wealth but the presence of tombs with equal wealth. If more archaeological evidence will help settle this debate in the future, the fact that humans were relatively egalitarian in the pre-Neolithic period (or much more egalitarian than the Neolithic societies) is so far the consensus among archaeologists.

[4] Please note that the term chiefdom and the classification of human societies in general is debated (Spencer, 1990) (see Currie and Mace 2011 for an evolutionary perspective). Without going in the details, the consensus is that societies with central authority emerge at the Neolithic transition.

and different layers or levels of hierarchy (Spencer, 1990). However, we focus in this thesis on the *emergence* of hierarchy and thus we constrain ourselves to the transition from egalitarian tribes to the first form of hierarchy, chiefdoms (although states will be discussed briefly for further work). A large diversity of complex social organisation can be observed in history but overall, hierarchy is the prevalent organisation. In the last millennia, egalitarian organisation still exists in small groups but is rarely observed in large groups on a long period.

For hundreds of thousands of years, hierarchy was almost absent in human societies. 12, 500 years ago, hierarchy started to spread all over the world. Today it is pervasive at any scale. What was the driver of such an impressive transition? It is hard to provide a simple answer mainly because the emergence of hierarchy appears as a paradox. Indeed, leaders enjoy preferential access to resources (Earle, 1987), a better health (Hatch, 1987; Marmot, 2005), and a higher number of mating partners (Zeitzen, 2008; Betzig, 1982). In short, the position of leader is more beneficial than the position of follower and such even when taking in account the cost of potential additional work done by leaders (Hayden and Villeneuve, 2010). Thus, why would any individual rationally accept a position of being a follower who might be exploited? The true puzzle of the emergence of hierarchy lies in solving this apparent paradox.

A first key to this problem lies in the other major change that happens at the Neolithic transition: the advent of agriculture. The general consensus is that the environmental changes brought by agriculture, kicked off the transition from equality to hierarchy (Price, 1995). However, this does not totally solve the puzzle because agriculture has led to numerous changes in the environment of humans, which can potentially explain the emergence of hierarchy. For instance, agriculture created defensible surplus resources (Smith et al., 2010; Bowles et al., 2010), increased group size (Bocquet-Appel, 2011; Aimé and Austerlitz, 2017) and reduced the mobility of individuals (Carneiro, 1970; Allen, 1997). To get further insight, we need to look at the roles and behaviours of leaders.

1.3 Coercive explanations for the emergence of hierarchy

A first possible explanation to the emergence of hierarchy is that followers do not have a choice. Dominance hierarchy can not be imposed by physical strength anymore, as seen in human ancestors, but it could be imposed by other means such as coercive institutions, e.g. taxes, army. Individuals could become dominant by building up economic and military power, which can then be used to get more economic and military power.

Coercive explanations see social organisation as the result of a tug-of-war between leaders and followers (Summers, 2005; Johnstone, 2000). The cognitive and technological innovations in hunter-gatherers would have tilted the balance of power toward followers, allowing them to create a reverse hierarchy. But agriculture would have restored the powers of leaders, even amplified these powers. On the one hand, agriculture created large surplus resources which can be stored and defended (Smith et al., 2010; Bowles et al., 2010). Freed from food sharing required to sustain a hunter-gatherer lifestyle, leaders would have taken advantage of surplus resources to build up dominance and control others with . On the other hand, agriculture led to sedentary lifestyle because farming is a process that benefits only in the long term. Thus, the cost of escaping a despotic leader for a more egalitarian organisation would have been much more important. With leaders controlling the most productive lands, followers would have been better off accepting the dominance of leaders (Carneiro, 1970).

Coercive explanations for the emergence of hierarchy propose that hierarchy is imposed by leaders using coercive means. But how to explain the emergence of hierarchy *in the first place* when any advanced form of coercion was absent? Despite leaders being freed from food sharing, it is unlikely that leaders could have established dominance using coercion in groups of partisans of equality. Much anthropological evidence shows that inequality was strongly limited in pre-hierarchical societies because of anti-authoritarian mechanisms, e.g. gossip, ostracisation; and the absence of coercive institutions, e.g. dedicated armies and tax collection (Boehm, 2001). One could argue that some lucky individuals would have accumulated enough resources without attracting undue attention of coalitions of equals. But it is unlikely knowing that for hundreds of thousands of years, coalitions of followers have imposed strong dominance on uprising leaders and successfully maintained equality (Boehm, 2001). Coercive theories can explain the maintenance of hierarchical societies but they struggle to explain the evolution of social hierarchy *in the first place*.

An alternative theory called the "iron law of oligarchy" proposes that in the absence of means to build up economic or military power, leaders have established their dominance by accumulating political power, i.e. influence over collective decisions (Michels, 1911). Leaders might exert their influence to leverage institutional rules and bias collective decisions in their favour, e.g. distribution of resources, command of military (Dahrendorf, 1959). This political power over collective decision could have been used to build up economic and military power, which then can provide coercive means to impose dominance.

This explanation still suggests that leaders have been able to monopolise the political power in the first place despite the careful watch of egalitarian members of the group. Functional theories propose that political power has not been stolen by leaders but it has been voluntary relinquished to them because centralising authority facilitates the group organisation. Whether it is to build an irrigation system, to plan a future battle or to vote a new law, each collective task requires participants to agree on countless decisions. As can be seen in ancient cooperative hunting (Skyrms, 2003) or in a modern share-holder meeting, leaders are strongly involved in organisation for instance assigning the role of each, settling arguments between decision-makers and helping to decide the future course of action (Calvert, 1992). The organisational benefit of hierarchy would have allowed the group to tackle more complex and more beneficial collective tasks, e.g. build a more elaborated irrigation system, win more battles, maintain cooperation at a larger scale by creating institutional rules (Ostrom, 1990).

1.4 Functional explanations for the emergence of hierarchy

Functional explanations see the emergence of leaders as voluntary and social hierarchy as an adaptation. Hierarchy would have resulted from the demographic explosion initiated by agriculture (Bocquet-Appel, 2011). Hunter-gatherer tribes are composed of hundreds of individuals whereas chiefdoms contain thousands of individuals. As a group grows, stresses build up on the decision-making because the number of decisions and the difficulty to take them also increase (Johnson, 1982). Leaders could have arisen in response to this scalar stress because leaders would facilitate group organisation (Calvert, 1992). Reviews of ethnographic data presents evidence that group size scales with political complexity, i.e. the number of political units, (Johnson, 1982; Carneiro, 1967), number of organisational traits (Carneiro, 1967) or probability of group fission (Alberti, 2014). On one side of the range, small-whale hunters have one single coach to coordinate group hunting (Friesen, 1999). On the other extreme, modern states or companies have dozens of politicians and managers who are fully dedicated to the task of organising.

The functional explanations for the emergence of hierarchy have the benefit of filling the gap of coercive theories because it provides an explanation for the emergence of hierarchy in groups initially egalitarian. However, the functional explanations are not straightforward. As mentioned before, leaders receive more resources and have more offspring than followers. Thus, it is still advantageous for an individual to be a leader rather than a follower, even if it is at the expense of the whole group capacity to organise. Why would an individual become a costly follower instead of letting his neighbour fulfilling this role? A functional emergence of hierarchy suggests that the group benefit brought by hierarchy would be enough to overcome individual pressure driving everyone to become a leader rather than a follower (Spisak et al., 2015). Yet, there is a conflict between individual and group interests which makes this condition not trivial (Frank, 1998; West et al., 2007).

1.5 An evolutionary investigation of the iron law of oligarchy

Coercive theories see social organisation as the result of the balance of power between leaders and followers. These theories explain the maintenance of hierarchy by leaders using economic power and coercive means to impose dominance and sustain the hierarchy. Yet, they overlook the beneficial role of leaders and struggle to explain the emergence of hierarchy in the first place. Functional theories see social organisation as an adaptation. These theories explain the emergence of hierarchy by the roles that leaders play in the group, which would have been amplified by the demographic increase brought by agriculture. Yet, they overlook the despotic role of leaders and apply in restricted conditions. The iron law of oligarchy unifies these two explanations. It states that political leaders arise to deal with the complexity of coordination as a group expands, therefore allowing these leaders to bias collective decisions in their favour (Michels, 1911) [5].

The iron law of oligarchy has the benefit of providing a comprehensive scenario for the emergence of hierarchy encompassing both the functional and despotic role of leaders. However, the generality of the iron law of oligarchy has been challenged by new evidence on human organisations (Leach, 2015). Criticisms stress that some assumptions of the iron law of oligarchy lack of justifications. For instance, it is not clear why centralising power would facilitate group organisation (Breines, 1980; Rothschild and Whitt, 1986) or why leaders would always become despotic (Edelstein, 1967; Schumpeter, 1942). Consequently, it is still not clear under which conditions the iron law of oligarchy holds. Further investigation of the iron law of oligarchy has been limited because this theory proposes a verbal model, which lacks of a more formal description. In particular, the iron law of oligarchy is a theory which describes changes in social organisation but is not grounded in a supported theory which describes how societies change.

To fill this gap, we need to examine in finer details where does social organisation come from. Social organisation is the reflect – an emerging property – of the behaviours of society members. It is because some individuals act as leaders and some individuals act as followers that there is a hierarchy. More precisely, human adaptation to hierarchy appeared under two forms (Pielstick, 2000), expressed in (i) human personalities (Judge et al., 2002), and (ii) human preferences. First, hierarchy can emerge from the fact that a minority of individuals have a leader personality and a majority have a follower personality. Leaders and followers are then defined by their intrinsic characteristics

[5] Please note that this theory or part of this theory might have been proposed by other authors (in particular in other fields). We still designate this explanation by the term iron law of oligarchy because it is the first and most known occurrence of such explanation, as far as goes our knowledge.

either physical, e.g. height (Berggren et al., 2010), or psychological, e.g. talkativeness, charisma (Judge et al., 2002). For instance, leader effectiveness is highly correlated with particular psychological traits such as openness and extroversion (Judge et al., 2002). This hierarchy where leaders and followers are defined by their intrinsic characteristics is called *informal* hierarchy. Second, hierarchy can emerge from cultural preferences toward institutional rules supporting hierarchy. In such case, leaders and followers are appointed by decision of the group or a subset of the group. For example, groups confronted by other groups in collective games explicitly elect and identify an individual as a leader (Sherif et al., 1954). We call this form of hierarchy *institutional* hierarchy to stress that it is supported by institutional rules, which are created by group decision and actively enforced by monitoring and punishment (Ostrom, 1990; Hurwicz, 1996). Thus, explaining the evolution of hierarchy is to explain (i) the evolution of leaders and followers behaviours, i.e. informal hierarchy and/or (ii) the evolution of preference toward hierarchy, i.e. institutional hierarchy.

Taking in account this detail is important because, if the rules governing how societies change are hardly known, the rules governing change in human behaviours are well described. The theory of evolution by natural selection (Darwin, 1859) and its modern synthesis are a set of theories which describes precisely the rules and processes governing the change in human behaviours, whether it comes from biological characteristics or cultural preferences [6]. Although other processes can lead to change in human behaviours, Darwin's theory of evolution is a critical paradigm to understand the changes in human behaviour because Darwinian evolution is the main driver of change on a long time scale (Rosenberg, 2017). In the recent years, there has been an extensive effort to incorporate social and political sciences theory within the evolutionary theory paradigm (Rosenberg, 2015; Mesoudi, 2011). Doing so has important benefits. First, it provides support to the studied social sciences theories by showing it can fit into the theory of evolution by natural selection, one of the most supported theories in biological sciences. Second, evolutionary processes can be rigorously described by mathematical rules and thus, can provide a formal exploration of social theories (Otto and Day, 2007). Last but not least, it provides key knowledge on evolutionary processes and in particular, how evolution behaves in social settings.

Before going further, it is important to review the evidence that the characteristics underlying hierarchy not only evolve but can also be selected. Selection is crucial because it is the evolutionary force which drives characteristics toward a certain direction. In absence of the conditions necessary for selection, Darwinian evolution can not be accounted for explaining the common trend observed in the evolution of social organisation. To be selected, the individual characteristics underlying hierarchy require to follow three rules (Lewontin, 1970):

[6] Cultural items replicate and thus evolve although with possible difference (Claidière, 2009; Claidiere et al., 2014).

- The traits need to vary. It is easily explained by the mutation process.
- The traits need to be heritable. Evidence indicates that the physical and psychological characteristics underlying leader and follower behaviours are partially heritable (Judge et al., 2002). The social position of leader is also partially heritable (Dal Bó et al., 2009).
- The traits need to modify the fitness, i.e. reproductive value. Evidence shows that leader positions are associated with higher income, resources and access to mate partners (Betzig, 1982; Earle, 1987; Hatch, 1987; Marmot, 2005).

Evidence supports that the social organisation of human group is partly the product of selection [7] (Van Vugt et al., 2007; Van Vugt et al., 2008; Van Vugt et al., 2011). It is important to note that it does not mean that social organisation has to be the result of *genetic* selection, but it can also be the product of *cultural* selection. The support either biologic or cultural of hierarchy is not our prior concern here, provided that the traits underlying hierarchy follow the rules of selection.

In conclusion, we propose in this thesis an evolutionary version of the iron law of oligarchy. The evolutionary iron law of oligarchy investigates the same scenario proposed by the iron law of oligarchy but it reinterprets this scenario in evolutionary terms. It takes in account the benefit and cost in term of reproductive success of the different traits of individuals. Doing so, it can provide the direction of selection forces driving the change in these traits and how different environmental factors affect it.

1.6 A main limit to evolutionary models of hierarchy: how to describe hierarchy at the individual level?

The evolution of hierarchy has been commonly studied using models. Models are simplified versions of reality, which focus only on important features of a system. They are widely used in evolution to study the different paths of evolving traits thanks to the simplicity of the mathematical rules underlying Darwinian evolutionary process (Otto and Day, 2007). They are particularly useful to study the evolution of human behaviours because they allow to reproduce past scenarios and bridge together the small pieces of evidence from past human history. Evolutionary models have been successfully developed to explore coercive theories (Johnstone and Cant, 1999) or functional theories, i.e. leaders as a monitors (Hooper et al., 2010), leaders as contributors (Gavrilets and Fortunato, 2014), leaders as managers (Powers and Lehmann, 2014). However, there is limited work on the scenario proposed by the ""iron law of oligarchy", either on the

[7] for extensive review see (Van Vugt et al., 2011).

evolution of leaders as coordinators, leaders using influence to create despotism or a combination of these two parts.

This gap can be explained by that to study the evolution of hierarchy requires to describe processes on different levels of abstraction, i.e. individual and group. For instance, hierarchy is a property of a group but behaviour is a property of an individual. Yet, both levels or how they relate need to be described. It is a well-known problem of multilevel evolutionary processes (Okasha, 2008): (i) how to describe a group-level trait in terms of the traits of its individual members, and (ii) how to link individual traits back to group fitness? Hierarchy is often described as a proportion of leaders and followers. But leaders and followers describe a large number of behavioural traits and it is difficult to pin down a particular one, which could explain the benefit they bring to organisation. The lack of description of hierarchy at the level of individual has lead to several gaps in the iron law of oligarchy. [8].

First, the immediate consequence of missing a description of leaders and followers is that the evolution of leaders and followers personalities, i.e. informal hierarchy can not be studied. Nonetheless, informal hierarchy does not require political institutions and thus is a strong candidate to explain the first emergence of hierarchy. Similarly, it is difficult to investigate the evolution of different forms of institutional hierarchy, which are often summarised as a discrete state of the group, e.g. absolute equality or absolute hierarchy. Second, the conflict between group benefit and individual cost and its role on the evolution of hierarchy can not be captured. Nonetheless, the main limit of functional theory lies in this assumption that the benefit that a leader brings to a follower is high enough to counterbalance the cost of being an exploited follower. Third, the absence of a description of hierarchy at the level of individuals means that the effect of hierarchy on group organisation has to be assumed. Nonetheless, the core postulate of the iron law of oligarchy is that leaders facilitate but bias collective decision-making. These effects are hard to measure but can be deduced from the micro-interactions between individuals during collective decision-making. Fourth, the competition between informal and institutional hierarchy has not been investigated. On one hand, informal hierarchy exists "by default". It emerges from the personalities of individuals without any need to enforce it. On the other hand, institutional hierarchies need to be actively created and enforced. For instance, individuals not respecting the decided hierarchy needs to be monitored and punished. Yet, institutional hierarchies are surprisingly pervasive in modern societies, given that they carry additional costs in comparison to informal ones.

To summarise, the lack of a description of hierarchy at the level of individuals results in a number of gaps in the investigation of an evolutionary version of the iron law of oligarchy:

[8] The lack of formal description of hierarchy and in particular “oligarchy” also has resulted in debates and confusions in political sciences, as researchers were using different definitions (Leach, 2005)

- There is no general model describing the effect of leader and follower on group decision-making.
- There is no investigation of the role of organisation to explain the evolution of informal hierarchy.
- There is no investigation of the competition between informal and institutional hierarchy.
- There is no investigation of the evolution of despotism and economic inequality from initially hierarchical but egalitarian groups.

1.7 Social organisation as a distribution of influence

In this thesis, we propose a new formalisation of leaders and followers, social organisation and social hierarchy. Taking inspiration from the iron law of oligarchy and previous works (Gavrilets et al., 2016; Johnstone and Manica, 2011), we define social organisation by the distribution of political power, i.e. the realised influence of an individual on group decision. We define *realised* influence as the weight of an individual's opinion on the group's decision.

Nonetheless, realised influence is not a biological or cultural characteristic, and thus can not evolve. Hence, we define individual by an intrinsic influence which summarises traits by which an individual is able to influence collective decisions [9]. This trait depends of the capacity of an individual to communicate its opinion and it summarises three traits: persuasion, talkativeness and stubbornness. We choose these three characteristics because we suppose that they are required for an individual to influence group decisions. Individuals with high intrinsic influence will keep their initial opinion (stubbornness), transmit it in a efficient way (persuasiveness) to a high number of individuals (talkativeness). On the contrary, an individual who is persuasive but not talkative will not spread their opinions above a few other individuals. Another example is a persuasive but not stubborn individual, who will not transmit their preferences but the last opinion they heard. In addition, these traits are observed in psychological profiles of leaders (Judge et al., 2002). We refer to intrinsic influence as influence because it is the main focus of the work presented here.

We define the social organisation of a group as the distribution of individuals' influence. Egalitarian to highly hierarchical groups are represented by an equal to strongly positively skewed distribution of influence.

This formalisation has several benefits:

[9] It is the same distinction that Johnstone and Manica (2011) do between intrinsic leadership (equivalent to intrinsic influence here) and effective leadership (equivalent to realised influence here).

- It captures a wide range of forms of hierarchy, from egalitarian to extremely hierarchical.
- It captures the continuous range of more or less leader like and follower like behaviours, e.g. from extreme leader to extreme follower.
- It is abstract enough to describe both informal and institutional hierarchy. The influence of an individual can result from its personality or group decision. For instance, an individual can have a high influence because he is more talkative or because his position gives him more opportunity to speak.
- If we restrain the range of organisation we are looking at, we can describe the social organisation of a group by one value, the skewness of the distribution of influence.

In this thesis, we claim that the influence is the major feature of leaders and followers, and that is sufficient to explain the evolution of both functional hierarchy and despotism under the conditions observed at the Neolithic transition.

1.8 Summary and research questions

Our thesis is that describing leaders and followers by their influence is enough to explain (i) how leaders facilitate but bias group organisation, (ii) the evolution of functional hierarchy with leaders as organisers and (iii) the evolution of despotism with leaders imposing inequality. The scenario for the emergence of hierarchy that we investigate is the following. The advent of agriculture led to an increase in group size and thus increased the benefit of hierarchy. The increase in group size drove the evolution of influential leaders and influenceable followers because they facilitate group organisation, and even more so in large groups. Once influential leaders and influenceable followers are in place, leaders had been able to bias collective decisions to monopolise resources and bias followers' opinions to avoid being punished by followers. Using this advantage, leaders evolved despotic behaviours and created economic equality. High levels of hierarchy would have been maintained by subsequent increases in group size and by leaders using their political and economic power to strengthen their position.

To investigate this scenario, we combine models of social dynamics, i.e. how individuals interact, and models of evolutionary dynamics, i.e. how individuals change with time. Because of the nonlinearities of the model, which result from the interactions of all of the variables, we analyse it using replicated individual-centred simulations.

The first gap to fill is to investigate if and how leaders could facilitate group organisation. We propose that leaders could reduce costs of organisation by reducing the time a group spend to reach consensus. The time spent to reach consensus is costly because groups that take too long to reach a decision may lose resources or eventually fail the collective task, e.g. no decision taken before a battle starts. Thus, we investigate the following question:

Research question 1. *Does a skewed distribution of influence within a group reduce the time to reach consensus?*

In Chapter 3, we mathematically describe collective decision-making by an opinion formation model, which consists of a sequence of discussions between individuals until a global consensus is reached (Castellano et al., 2009). We extend this model to integrate leaders and followers, defined by different values of influence.

We demonstrate that a skewed distribution of influence is enough to reduce the time to reach consensus and scalar stress, i.e. the increase of time to reach consensus as group size increases. In addition, hierarchy with an influential single leader leads to bigger reductions in (i) the consensus time, (ii) the variation in the consensus time, and (iii) the increase in consensus time as group size increases.

Even if social hierarchy facilitates group organisation, it is not clear if this benefit can overcome the selection pressures driving everyone to become a leader instead of an exploited followers. This leads us to the next question:

Research question 2. *Can the organisational advantage of a skewed distribution of influence drive the evolution of individuals toward leader and followers behaviours even if it creates inequality?*

In Chapter 4, we develop an evolutionary model where influence is an evolving trait. The population is structured in patches and within a patch, individuals organise together to produce a collective good. We integrate the previous opinion formation model to describe the collective decision-making of groups. The time to reach consensus determines the cost of organisation, and the realised influence of an individual on the final decision determines that individual's share of the collective good, i.e. influential individuals receive more resources.

We demonstrate that leaders and followers behaviours, i.e. informal hierarchy can evolve *de novo* in the presence of low initial inequality and increasing returns to scale [10], which are two reasonable assumptions for small-scale societies as observed before the Neolithic transition

The emergence of institutional hierarchy, i.e. chosen leader, can also be explained by the fact that it reduces costs of organisation (Powers and Lehmann, 2014). However,

[10] Increasing returns to scale describes the fact that an increase in the scale of an operation (here group size) is translated into a superlinear increase in the benefit produced by the operation Pindyck and Rubinfeld, 2001

institutional hierarchies are surprisingly pervasive in modern societies, given that they carry additional costs in comparison to informal ones. We propose that a key to this puzzle lies in the particularity of institutions which allow humans to hand-tune their behaviours and create single-leader hierarchy, in comparison to informal hierarchies in which leaders emerge through evolutionary processes. Thus we ask the following question:

Research question 3. *Can the organisational advantage of single leader hierarchy drive the evolution of preferences toward institutionalised hierarchy despite the additional cost of institutions?*

In Chapter 5, we extend the previous evolutionary model such that individuals can choose between informal social organisation where the influence of individuals is defined by individuals' characteristics, or institutional social organisation where the influence of individuals is defined by the institution. Individuals evolve both personality and preferences toward institutions.

We demonstrate that individuals evolve cultural preferences towards institutional hierarchy because (i) it provides a greater organisational advantage than informal hierarchy, (ii) reduces the detrimental effect of group size on the time to organise collective action and (iii) is more resilient in the face of inequality.

In both previous models, the development of social hierarchy creates inequality because influential leaders bias the decision and hence receive a higher share of resources. But even if leaders have a higher influence on collective decisions in hierarchical societies (Gavrilets et al., 2016), their despotic behaviours should be constrained indirectly by the satisfaction of the rest of the group. We propose that the large influence of leaders provide them with a mean to bypass the watch of followers and create larger level of inequality. Thus, we investigate the following question:

Research question 4. *Does a centralised social network structure lead to the evolution of despotism in hierarchical societies ?*

In Chapter 6, we build an evolutionary model where individuals are explicitly organised in a network structure either random or centralised with a leader as central node. Individuals are described by their preferences on the distribution of resources, and their opinions on the actual level of fairness in the society. We simulate the evolution of their distribution preferences and study how the network structure affects the level of despotism.

We demonstrate that a transition from equality to despotism will happen in presence of (i) highly influential individuals with a preferential access of resources; and (ii) weakly connected followers. This is because influential leaders are able to bias

followers opinion, thus jeopardising the followers' capacity to monitor and punish despotic leaders.

In Chapter 7, we summarise our results. We show that our contributions combined to previous works provide a strong theoretical support behind an "evolutionary iron law of oligarchy". We present further work to extend this theoretical work and to experimentally test our predictions. Finally, we discuss how this work contributes to our understanding of the evolution of social systems but also provides keys to design large self-organised artificial societies.

1.9 Publications

Portions of this thesis have appeared in the following peer-reviewed publications:

- Cedric Perret, Simon T.Powers and Emma Hart, *Emergence of hierarchy from the evolution of individual influence in an agent-based model*, Proceedings of Artificial Life Conference 2017, MIT Press, 2017

- Cedric Perret, Simon T.Powers, Jeremy Pitt and Emma Hart, *Can justice be fair when it is blind? How social network structures can promote or prevent the evolution of despotism*, Proceedings of Artificial Life Conference 2018, MIT Press, 2018

- Cedric Perret, Emma Hart and Simon T.Powers *Being a leader or being the leader: The evolution of institutionalised hierarchy*, Proceedings of Artificial Life Conference 2019, MIT Press, 2019

In addition, portion of this thesis has been submitted as:

- Cedric Perret, Emma Hart and Simon T.Powers, *From disorganised equality to efficient hierarchy: How does group size drive the evolution of hierarchy in human societies*, Proceedings of Royal Society B: Biological sciences. Submitted in 2020

1.10 Code availability

The code used for the models in this thesis is available on repositories at: "https://github.com/CedricPerret". The code for:

- Chapter 3 is available at "https://github.com/CedricPerret/ConsensusMod".

- Chapter 4 is available at "https://github.com/CedricPerret/EvolLeadMod".

- Chapter 5 is available at "https://github.com/CedricPerret/Institutional-Hierarchy".

- Chapter 6 is available at "https://github.com/CedricPerret/EvolDespotMod".

Second Chapter

Theories of the evolutionary origins of hierarchy

The emergence of social hierarchy has been thoroughly studied. Proof shall be in the multitude of theories proposing their explanations for the origin of hierarchy. In this chapter, we give an overview of the most supported theories of evolution of hierarchy. We aim to give the reader a grasp of the past and current state of research on the evolution of hierarchy and shed light on the gaps that the theory explored in this thesis fulfils.

This chapter is organised as follow. First, we describe what theories of evolution of hierarchy are trying to explain and model. To do so, we present the important features of the event that we aim to explain (the explanandum) – the transition from egalitarian to hierarchical societies – and the features of the event which is used to explain (the explanans) – the environmental changes brought by the advent of agriculture. We then describe how previous theories have connected these two events together. We divide the theories into two parts, coercive theories and functional theories. Coercive theories focus on the despotic side of leaders. They suggest that hierarchy emerges because leaders use coercive means to impose dominance on the rest of the group. Functional theories focus on the beneficial role fulfilled by leaders. They suggest that group members voluntarily adopt hierarchy because of the benefit it brings to them. Coercive and functional theories each explain one facet of hierarchy, but overlooks the other. We describe how a theory from political sciences – "the iron law of oligarchy" – can fill these gaps and unify coercive and function theories. We propose to investigate this theory with an evolutionary perspective and we describe how doing so can answer the criticisms on this theory. Finally, a major gap in an "evolutionary iron law of oligarchy" is the lack of a microscopic description of the role of leaders on group organisation, i.e. how leaders help the group organise. We show how the field of social dynamics can fill this gap and provide a new view on previous theories of evolution of hierarchy.

2.1 Archaeological and anthropological evidence on the Neolithic transition

The first step to build a theory is to identify and define what the theory is trying to explain. Theories on the evolutionary origins of hierarchy have aimed at connecting the two main events of the Neolithic transition (i) the emergence of hierarchy and (ii) the environmental changes brought by agriculture. In this section, we present the important features of these two events.

First, let settle down possible confusion on the term ”transition” in Neolithic transition. The Neolithic transition was not a sudden change which happens in all groups around the world. In truth, the Neolithic transition was spread on thousands of years and happened at different periods for different regions of the world. For instance, agriculture emerges at different time for different human population (Diamond, 1997), e.g. the domestication of rice in China is considered to have happened along 5000 years (Jones and Liu, 2009); and the transition from hunter-gatherer to farming was progressive, e.g. some groups relied on a mix of hunting, gathering and farming (Smith, 2001). There is also a a number of places where human groups still live as egalitarian hunter gatherer. However, we talk about Neolithic *transition* because we observe a clear shift from egalitarian hunter-gatherers to hierarchical agriculturists in the majority of human societies, and that in a short time on the scale of archaeological time.

2.1.1 The Neolithic transition and the emergence of social hierarchy

The Neolithic transition marks the emergence of hierarchy and leadership in human societies. However, depending of the definition used, leadership is considered already present in animals, in hunter-gatherers, or present only later in modern complex societies. Indeed, hierarchy and leadership have been studied by a wide range of scientific fields. From social sciences to evolutionary biology through to multi-agent systems, the semantics employed vary widely. In this section, we precise the important features of the hierarchical societies emerging at the Neolithic transition and how they differ to other notions of leadership found in the scientific literature.

2.1.2 The *explanandum*: Leaders of post-Neolithic societies

2.1.2.1 Features of leaders of post-Neolithic societies

In brief, the Neolithic transition describes the emergence of leaders which:

- possess a higher amount of resources;
- have some form of control on other individuals;

- are permanents, i.e. the two previous features are present for most of the life of the leaders;

The association between inequality of wealth and hierarchy is well known (Flannery and Marcus, 2012; Hayden, 2001). Written records from ancient societies already present disparities in resources distribution and reproduction (Betzig, 1993; Boone, 1992). Comparative and ethnographic studies of recent societies also reveal dramatic examples of despotism and differential reproduction (Casimir and Rao, 1995; Betzig, 1982). This inequality can be expressed in different manner. First, the most obvious inequality of resources is inequality of wealth. Post Neolithic leaders all exhibit disproportional amount of wealth (Earle, 1989). In the tribes of Northwest coast of North America, one fifth to one half of all food produced are surrendered to chiefs for the purpose of redistribution during feasts. In reality, considerably less was redistributed than was received (Ruyle, 1973). Hayden and Villeneuve (2010) finds similar results on Futuna and other Polynesian islands. The inequality can also be expressed in access of mating partners (Zeitzen, 2008; Betzig, 1982). For instance, in Amazonian Indian tribes, polygamy is an exclusive privilege of leaders and a sign of their power. Finally, this inequality can also be expressed more indirectly, for instance in rights. In the Polynesian islands, only the chief and their families have the right to construct the larger canoes used for inter-island trade (Hayden, 2001). Ultimately, these benefits are all translated into an evolutionary benefit. Leaders have a better chance of survival and a higher number of offspring.

Second, leaders in post Neolithic societies have some sort of control on other individuals. It can be that leaders can influence others' behaviours, punish them, or take decisions for the group. Often, leaders use this power to facilitate collective action. For instance, leaders can use their powers to punish defectors and enforce cooperation among members of the group (Kracke, 1978), solve conflict between individuals (Glowacki and Rueden, 2015) or coordinate individuals (Calvert, 1992). One of the most emblematic examples is the whale hunters of Lamalera Indonesia (Alvard and Nolin, 2002). To capture such big game, alone is impossible. Hunters spread on different boats and cooperate during an extended period of time to finally capture the whale. Each boat activities are organised by one man, who acts as a coach or manager (Alvard and Nolin, 2002). It is worth noting that this power can be used for the benefit of the leader rather than for the benefit of the group. In other words, the inequality of power and the inequality of resources are often related. For instance, in Zulu, leaders had the right to accuse any individuals for offence and punish the guilty individuals by appropriating cattle, then increasing its wealth (Krige, 1950). Interestingly, in Zululand, offences defined a wide range of action including partaking of first fruits before the king had tasted them, coughing, spitting, or sneezing while the king was eating.

The Neolithic transition is a transition from an equal distribution of wealth and power to an unequal distribution of wealth and power, which is concentrated in few permanent leaders.

2.1.2.2 What does this thesis not talk about? Other notions of leadership in the literature

The topic of leadership and hierarchy has been widely studied and thus, the terms had been defined differently across fields. In this section, we present the differences between the notion of leadership studied here and other definitions of leadership found in the literature knowingly in animals, in pre-Neolithic societies and in states (for a short review of the different notions of leadership, we advise the first part of Garfield et al. 2019b).

First, the term "leaders" is sometimes used to describe some individuals which have temporary authority in pre-Neolithic societies of hunter-gatherers (Von Rueden and Van Vugt, 2015). However, these leaders have two main differences with leaders of post-Neolithic societies. First, leadership in hunter-gatherer tribes is situational and facultative. In other words, a large number of group decisions were taken without any leaders. When there was a leader, its power was confined to a particular task or context, i.e. the best hunter might lead during hunting but does not get to decide how to distribute the hunted game. For instance, the !Kung of the Kalahari Desert are egalitarian but they recognised leaders during camp moves (Marshall, 1960). The Tsimane foragers elect individuals to represent their communities but their position hold in average for 5 years (but sometimes short as few months) (Von Rueden et al., 2014). The second important difference between the leadership before and after the Neolithic transition is that leaders in hunter-gatherer tribes did not receive or accumulate a large amount of resources (Woodburn, 1982; Boehm, 2001). Following on the same example, the Tsimane foragers have leaders during collective fishing. Yet, these leaders do not receive a higher share of the fish stock (Von Rueden et al., 2014). These differences lead to fundamentally different problems when looking at leadership in tribes of hunter-gatherers or in chiefdoms. For instance, the origin of followers in hunter-gatherer tribes is not a paradox because followers do not receive less resources than leaders. Actually, the question is sometimes reversed with the problem being why some individuals act as leaders if they do not receive more resources to compensate the costs of their extra work (Von Rueden and Van Vugt, 2015; Price and Van Vugt, 2014)? In addition, there is a clear benefit for individuals to follow the most knowledgeable individual as seen in hunter-gatherers. However, it is harder to explain why individuals would follow a leader in post-Neolithic hierarchies, where the leader might take decision on a large range of diverse topics, even if they have a limited knowledge on these topics.

Second, the term "leadership" is sometimes used to describe particular individuals in animal groups exhibiting collective behaviour. However, most examples of leadership in non-humans describe an emerging property in a particular context rather than a permanent social organisation. For instance, leaders can describe the first movers during swarming or migration events (Couzin et al., 2005; Garland et al., 2018). Some animals exhibit leadership which shares interesting features with human leadership (Conradt and List, 2009; Smith et al., 2016). For instance, primates are organised in dominance hierarchies where one individual can get more resources and thus a better chance of survival (Sapolsky, 2005). The African wild dog (*Lycaon pictus*) uses sneezing to vote on the departure of the group and recent research suggests that dominant individual initiates the depart faster than others (Walker et al., 2017). Yet, such forms of leadership can be explained by differential energetic demands (the most hungry moves first), asymmetry of information, division of labour and physical dominance. These explanations are not enough to explain such permanent and pervasive leadership as observed in human societies after the Neolithic transition. In addition, the parallel between animals and humans is often limited as humans differ by having cumulative cultural evolution (Dean et al., 2014), language (Berwick and Chomsky, 2016), advanced cognitive capacities (Hill et al., 2009), cultural niche construction (Laland and O'Brien, 2011), and large-scale cooperation (Bingham, 1999).

Third, it would be tempting to take current societies as a good example of hierarchical societies. However, we constrain the study presented in this thesis to the emergence of the first form of hierarchy in human societies. The hierarchy studied here (usually called chiefdoms in anthropology Service 1962) is characterised by a single layer of authority. Modern societies have much more complex form of hierarchy (usually called states in anthropology Spencer 1990) with multiple layers of authority, strong institutionalisation of the hierarchy and specialised administration. Explaining the emergence of states is a crucial topic but we believe that it requires to first understand the emergence of simpler and earlier forms of hierarchy. We also do not discuss the literature in leadership studies, e.g. contingency leadership (Fiedler, 1964), transformational leadership (Bass, 1990); which aims to understand the effects of different forms of leadership on modern organisations rather than the emergence of leadership itself.

In this section, we have defined the important features of the hierarchical societies observed after the Neolithic transition. We now review the other major event of the Neolithic transition: the advent of agriculture.

2.1.3 The *explanans*: The environmental changes brought by the advent of agriculture

The main candidate to explain the emergence of hierarchy is the advent of agriculture (Price, 1995) because (i) the transition in social organisation is correlated with the development of agriculture and (ii) agriculture led to many environmental changes. Different theories have looked at different environmental changes brought by agriculture to explain the transition in social organisation. These environmental changes are:

- Increase in population size. The Neolithic transitions marks a huge increase in the demography, for instance reflected in cemetery data (Bocquet-Appel, 2011) or genomic data (Aimé and Austerlitz, 2017). [1]

- Increase of cost of migration. Agriculture requires long term investment and daily maintenance (Carneiro, 1970; Allen, 1997). Thus, agriculture goes along with a transition from nomadic lifestyle to sedentary lifestyle.

- Emergence of surplus resources, which can be stored, defended and transmitted (Smith et al., 2010; Bowles et al., 2010). Unlike hunting game which needs to be consumed quickly, products of agriculture can be conserved and stored. The capacity to store resources has also been developed by the emergence of storage technology. The surplus resources can be used for trade, and later on, allows the development of advanced form of division of labour and craft specialists, e.g. potters, blacksmith. It is worth noting that the surplus resources brought by agriculture might have been limited at the beginning because of the high labour cost of agriculture (Bowles, 2011).

A complete theory explaining the evolutionary origins of social hierarchy should be able to provide a chain of causal links which connects the environmental changes of the Neolithic to the changes in social organisation. The next section will now review the theories which have pursued this goal and present the results of the main models built in support.

2.2 Evolutionary theories on the origin of hierarchy

In this section, we present the different theories explaining the evolution of social hierarchy and leadership. We focus but not restrain ourselves to literature presenting theoretical models of the evolution of leadership. This is because first, models provide the backbone of theories by presenting and investigating a chain of causal links. Second, we look at evolution because there is strong evidence for hierarchy being partly the result of evolution (Van Vugt et al., 2011) and because we are interested in the ultimate causes of the emergence of hierarchy rather than proximal and particular mechanisms

[1] The demographic increase of the Neolithic transition has been first attributed to the higher productivity of agriculture, which produces substantially more per unit of space than hunting (Bocquet-Appel, 2011). However, this explanation has been recently challenged as agriculture also has a high labour cost (Bowles, 2011) and health cost (Cohen and Crane-Kramer, 2007). The positive effect of agriculture on group size might lie in social aspects of farming, with for instance a reduction in the costs of child rearing.

[2]. To connect the two major changes of the Neolithic transition, researchers have looked closer to the behaviours of leaders. Leaders have two ambiguous facets, one despotic side and one beneficial side. In a logical way, the theories built have followed the same tendency and are mainly separated in two opposite arguments: the coercive and the functional theories.

2.2.1 Coercive theories

Coercive theories (also called conflict theories) focus on the despotic facet of leadership. They propose that hierarchy is imposed onto the group by dominant individuals using coercive means such as physical dominance or coercive institutions (Summers, 2005; Earle, 1989). To explain the transition from egalitarian individuals to submitted followers, coercive theories focus on the appearance of surplus resources brought by agriculture. This section presents the approaches and results of the major coercive theories: territorial circumscription, economic defensibility, patron-client and reproductive skew.

2.2.1.1 The territorial circumscription theory

Territorial circumscription is a major coercive theory advanced by Carneiro (1970). Using anthropological evidence, Carneiro (1970) claims that hierarchy occurs under circumscribed conditions when one group manages to conquer, incorporate, and then exploit the labour of another. A circumscribed environment is defined as favourable environment, e.g. fertile lands or abundant fishing spots, delimited by unfavourable environment either for ecological reasons such as mountains and desert — ecological circumscription (Carneiro, 1970) — or social reasons such as high density of neighbours villages — social circumscription. Because of such limits, the inhabitants of villages submitted by war can not escape the invaders or at least, have a higher benefit by staying in the favourable environment despite being exploited. Because the newly submitted lands and villages need to be governed, an upper class of leaders is created from the individuals of victorious villages. The lower class appeared from the prisoners of wars. Carneiro (1970) claims that potential surplus is present in fertile lands but not exploited before upper class force surplus production through taxation. The surplus resources are then used to attract other workers and artisans forming the rest of the society. To support this claim, Carneiro (1970) compares the Amazonian agriculturists with no political unit - living in large space of cultivable land - and hierarchical Peruvian coast villagers - living in a favourable environment surrounded by deserts and mountains and

[2]Proximate causes are the immediate and closest causes responsible for an event. Ultimate causes are historical explanations, which via proximate causes, led to the event (Mayr, 1993). In biology, it is considered that ultimate causes explain biological traits by the evolutionary forces acting on them, and proximal causes focus on physiological and environmental factors (for an overview of different type of explanation in biology, see Tinbergen 1963).

social stratification. Kennett et al. (2009) extend the theory by using an ecological model, which simulates the distribution of habitats to individuals. The authors apply this model to archaeological data describing population on California's Northern Channel Islands during an extended period (3000 -200 BP). They find that the distribution of habitat fits better the ideal despotic distribution rather than the ideal free distribution. In addition, they identify the origin of hierarchy concomitant to severe droughts (environmental circumscription) along with violent conflicts between villages. Similar approaches can be found in literature which incorporate evolution (Arnold, 1993; Dye, 2009).

The territorial circumscription underlies an important mechanism. The level of despotism is controlled by the capacity of followers to avoid domination, here the capacity to escape the dominant. They show that this capacity is a function of the cost of migration, which itself depends of the environmental factors and population pressures. However, evidence on such extreme despotism born only from warfare are rare. Filling this gap, some scientists proposed economical means as an alternative way for leaders to build its domination.

2.2.1.2 The economic defensibility and patron-client theories

Models of economic defensibility and patron-clients both support the idea that leaders build domination by monopolising economic opportunities. This theory was first developed by economic defensibility models based on anthropological data and ecological models (Boone, 1992; Brown, 1964; Dyson-Hudson and Alden Smith, 1978). It was proposed by Brown (1964) that the defensibility of resources, i.e. how much resources can be defended, is one of the most important determinants of territorial behaviours. According to a similar model, territoriality is expected to occur when critical resources are sufficiently abundant and predictable in space and time, so that costs of exclusive use and defence of an area are outweighed by the benefits gained from resource control (Dyson-Hudson and Alden Smith, 1978). Defensible, abundant and predictable are three features of resources brought by agriculture. Boone (1992) later applied this theory to hierarchy by modelling the dynamics of group formation. This work shows that followers would join despotic groups if unoccupied territory no longer exists. Particular individuals would exploit the lack of alternatives, as leverage to gain control of resources at the expense of other. This results in a hierarchical social organisation based on unequal access to resources.

The patron-client theory expands this work by showing how an initial inequality of resources can be reinforced — or put in the words of Percy Bysshe Shelley, how "the rich gets richer and the poor get poorer" (In *A Defence of Poetry*). Following a similar line of thought than economic defensibility theories, patron-client theories claims that hierarchy appears first from spatial variation in resources and land productivity (Smith and Choi, 2007). They add that initial inequality can be exacerbated because some individuals (patrons) use their economic resources to develop the loyalty of followers (clients) and receive back benefits under the form of labour or other support (Eisenstadt and Roniger, 1980; Chabot-Hanowell and Smith, 2012; Smith and Choi, 2007). In the long term, the labour produced by followers secures the economic power of leaders and leads to institutionalised leadership. Patrons can also use their economic power to build up their dominance, through alliance formation with leaders of other groups. Patron-client theories stress that the variation in economical power can come from any resources such as technological innovation (Roscoe, 2006; Ames, 2003; Arnold, 2010) or trading networks (Chabot-Hanowell and Smith, 2012).

Economic defensibility and patron-client theories show how inequality in habitat quality can become inequality of resources and get later reinforced by exchange of wealth and labour. However, they consider that inequality first appears because of the patchiness of habitat, despite this variation between habitat being already present before the Neolithic transition. The appearance of surplus resources could answer this point but it is still hard to see how some individuals would have accumulated large amount of resources in a group of egalitarian zealots. Before coming back to this critic, we present a more general coercive theory which integrate these explanations and factors in a broader framework: the reproductive skew theory.

2.2.1.3 The reproductive skew theory

The previous models have been expanded by a generalised theory: the reproductive skew theory. This theory focus on the “distribution of reproduction”, which describes how much the offspring of a generation is produced by the individuals from previous generation. It ranges from each individual having an equal number of offspring to one individual producing all the offspring. The “reproductive *skew*” describes the skewed distribution of reproduction in a group either due to direct inequality, e.g. access to mates or indirect inequality, e.g. access to resources (Keller, 1994).

Models of the reproductive skew theory study the evolution of traits of a dominant individual which modulates its exploitation of followers. On the one hand, increasing its exploitation of followers provides more resources and thus a higher reproductive success. On the other hand, reducing its exploitation of followers can be beneficial because it provides to followers staying incentives (reproduction conceded to subordinates to prevent their departure) or peace incentives (reproduction conceded to subordinates to prevent them from fighting for supremacy with the dominant). Reproductive skew models can then calculate the skewness of the reproduction distribution – the level of inequality – by looking at the value of the traits which maximise the inclusive fitness of the dominant, i.e. its fitness and fitness of related individuals.

These models were first developed by Vehrencamp (1983) and inspired by previous arguments concerning the conflicting relationship between followers’ options for dispersal and the ability of dominants to monopolise reproduction (Alexander, 1974). Later works expand the model of Vehrencamp (1983) and be categorised in two categories: transactional models and compromise models. Transactional models focus on the trade-off between exploitation by the dominant and groups stability (for review see Buston et al. 2007). Transactional models consider that leaders have some form of control on followers. However, the leader has to temper its domination to prevent the departure of followers. That is because the departure of followers from the group reduces the total productivity of the group, and ultimately the absolute amount of resources extracted by the dominant. The level of reproductive skew depends on the reproductive benefits of being in a group, the ecological constraints and the relatedness between the dominant and followers (Johnstone, 2000). The second type of model, compromise models (or tug-of-war models), focuses on the trade-off between exploitation by the dominant and cost of conflicts. Compromise models estimate that the dominant have a limited ability to impose its domination and thus, the skewness of the reproduction distribution is a compromise depending of the ability of dominant and followers to impose their interests (Cant, 1998; Reeve et al., 1998; Buston and Zink, 2009). In these models, the relative competitive ability of the followers and the relatedness between the dominant and followers are the main determinant of the distribution of the reproduction.

Johnstone (2000) suggested a synthetic perspective that combines considerations of group stability (as in transactional models) with the struggle for the control of reproduction (as in compromise models). Its result indicates that the conclusions of previous models are bound to vary in relation of the the extent of dominant control, the threat of departure and the possibility of eviction.

In short, reproductive skew theory sees social organisation as the equilibrium state between (i) the capacity of the dominant to appropriate resources and mating partners and (ii) the capacity of followers to avoid the domination. Reproductive skew models have been able to synthesise previous coercive theories into a generalised framework to study the evolution of despotism. We have presented here few of their key methods and results but more extensive reviews can be found (Summers, 2005; Johnstone, 2000; Keller, 1994). To summarise, reproductive skew theory predicts that the level of inequality is dependant to the:

- ecological constraints and opportunities for independent breeding;
- group productivity as a function of group size;
- genetic relatedness of group members;
- the fighting abilities of dominants and followers;

Reproductive skew models have the benefit to clearly link the different environmental factors to the level of inequality. They do that by using a formal mathematical approach grounded in the theory of evolution. However, reproductive skew models have been criticised because of the lack of consensus in their predictions. For instance, two subtypes of reproductive skew models (concession models Vehrencamp 1983; Reeve and Ratnieks 1993 and restraints models Johnstone and Cant 1999) yield opposed predictions on the effects of group productivity benefits, opportunities for independent breeding and relatedness on inequality (Johnstone, 2000). In addition, some of the predictions have either failed to be supported by data, or found hard to test because of the difficulty to measure some factors in real world (Nonacs and Hager, 2011). Finally, their applicability to human societies is limited. In particular, reproductive skew models often consider groups of two when Neolithic societies could go up to thousands of individuals. As an example, reproductive skew models usually assume that followers have complete information on their benefit to stay in the group, which is very unlikely in large groups. When Kokko (2003) relaxed the assumption of complete knowledge, the evolutionary stability of reproductive skew models disappeared.

2.2.1.4 Coercive theories: summary

Coercive theories state that despotic hierarchy is the result of coercive domination by leaders. The level of despotism is determined by the capacity of the leaders to impose this domination by using physical dominance, economic control and coercive institutions and the capacity of followers to avoid this domination by leaving the group or fighting against the dominant. Coercive theories shed light onto a major mechanism and successfully encompass one facet of leadership. However, coercive theories fail to explain how some individuals acquired such power in the first place. Coercive theories usually advance the argument of inequality being already present in the quality of habitats but then why such inequality was not present in pre-Neolithic egalitarian hunter-gatherers? This paradox is commonly solved by the advent of agriculture which led to the creation of defensible and transmissible surplus resources. Yet, if the leaders use surpluses to build up control, it is hard to see why followers would not have stopped them. The development of hierarchy appears before institutions of coercion such as military or police, and follows a long period where followers successfully controlled the dominant individuals. In addition, the high labour cost of the first form of agriculture would have limited the proportion of surplus available (Bowles, 2011). As a result, coercive theories seem to not fully explain the evolution of leadership but only the transition from hierarchy to despotism. Indeed, they fail to explain the emergence of beneficial leaders despite this facet being backed up by empirical evidence (Van Vugt et al., 2007; Van Vugt et al., 2011). Interestingly, the theory advanced by Carneiro (1970) states that leaders have appeared because large groups needed to be organised. Chabot-Hanowell and Smith (2012) also argues that group resources defence is a collective action problem. Wittfogel (1957) proposed in its hydraulic empire hypothesis that hierarchical government structure emerges through the need of central coordination to control irrigation systems and floods. Many coercive models recognise leaders emerging because of the benefit they brought to the group, although they do not elaborate on this aspect. This facet of leadership has been well explored by the second type of theories: functional theories.

2.2.2 Functional theories

Functional theories (or voluntaristic theories) focus on the manager facet of leadership. They propose that hierarchy is a mutually beneficial system between leaders and followers (Service, 1975; Diehl, 2000; Van Vugt et al., 2011). The costs of exploitation by leaders are balanced by the greater benefits that leaders provide as organisers, monitors or contributors. To explain the transition from egalitarian to hierarchy, functional theories focus on the demographic increase resulting from the advent of agriculture and the new social challenges it brought. We review here the models which assume that the beneficial roles of leaders have been the driver of evolution of leadership [3]. It is worth noting that it also encompasses models which consider despotic leaders but that do not focus on this facet.

2.2.2.1 Leaders contribute to the public good

An important part of the success of human groups rely on their capacity to cooperate to produce and manage public goods. Leaders with their large amount of wealth, could be a valuable asset to the production of these public goods. Gavrilets and Fortunato (2014) have developed a model studying how inequality of resources affects the contribution of individuals to a collective action. They show that in unequal groups, leaders benefit to the group by contributing a large part of the effort required to produce resources. This is because leaders compete with leaders of other groups during intergroup conflicts. Leaders in groups which successfully tackle collective task, have a higher chance to win and thus, to get a higher fitness than other leaders. Yet, the model does not investigate the evolution of hierarchy by itself but rather how inequality can solve social dilemma in collective action problem. It is still not clear how this form of inequality would have evolved in the first place.

2.2.2.2 Leaders monitor and punish defectors

A major difficulty in large social groups is to maintain cooperation between individuals (Powers and Lehmann, 2017). A subset of functional theories proposes that leaders

[3] Please note that we did not integrate the theory of *service-for-prestige* in this review (Price and Van Vugt, 2014). This is because the contribution of this theory is to explain the presence of leaders in small-scale societies, rather than leaders as observed in post-Neolithic societies. This theory proposes similar processes than coercive theories to explain the emergence of leaders with higher amount of resources, knowingly the capacity of followers to leave the group or to fight back the leaders.

maintain cooperation by monitoring and punishing defectors. Indeed, punishment of defectors is an efficient method to maintain cooperation within a group (Boyd and Richerson, 1992). However, punishment itself has a cost and it is advantageous for an individual to let other individuals pay this cost. It leads to a second order free-rider problem, and can lead to the disappearance of punishment and cooperation (Fowler, 2005).

Hooper et al. (2010) built an evolutionary model where leaders play a role of monitors and punishers [4]. Using an evolutionary game theory framework, the authors show that a supervising leader is a preferred solution to the problem of free riding in large cooperative groups. In other words, an increase in group size as observed at the Neolithic transition would lead to the transition from mutual monitoring to appointed monitoring. This can be explained by individuals abandoning mutual monitoring and mutual punishment in large groups because group size dilutes the individual benefit of punishment. In large groups, paying fee to a leader is a less costly mean to enforce cooperation and enjoy its benefits.

In the model of Hooper et al. (2010), leaders accept to pay the cost of punishment because they are compensated by a higher share of the public good produced. This results in leaders having a final similar pay-off than other members of the groups. Later on, Hooper et al. (2015) expand his model to take in account ecological factors and show that their previous results hold even with inequality. In a similar way, Smith and Choi (2007) have developed a model where leaders are appointed monitors and compared it to a patron-client model. They find that both scenarios are capable of producing hierarchy with marked and stable inequality in resources.

These models of evolution of leadership and monitoring show that leaders can be a solution to maintain cooperation. Hierarchy would emerge because followers benefit from the cooperation enforced by leaders. However, it is still hard to conclude how much this explanation applies in real world. First, evidence contests the prevalence of costly punishment to enforce cooperation in human societies (Guala, 2012). For instance, hunter-gatherers prefer to stop interacting with defectors rather than punishing them directly (Baumard, 2010). Second, a recent analysis of a large set of anthropological studies did not find strong evidence for the role of leaders as sanctioning free-riders (Garfield et al., 2019a). Third, appointed monitoring could also be limited by high group size. Indeed, the capacity of a leader to monitor everyone is clearly limited by the size of the group and surely impossible in large post-Neolithic societies. Evidence shows that human tend to choose a more economic way by creating set of rules also known as institutions (Ostrom, 1990). These rules are often designed in a way that monitoring is easily done by other individuals and the punishment is enforced by a specific group of individuals. Although leaders are present at the head of the punishing institutions, their

[4] This model has also been extended in an agent-based model and successfully tested on anthropological data describing Pueblo societies of the northern US Southwest (Kohler et al., 2012)

involvement in the task itself are usually limited to managing these institutions. In the same vein of evidence, another major part of the literature proposed that leaders fulfil another role: organisers.

2.2.2.3 Leaders organise collective actions

Even if individuals are willing to cooperate, they need to agree how. Collective actions, e.g. to hunt in group, to build a monument or to fight in a battle, require that individuals coordinate their actions (Cooper, 1999). For instance, a group needs to decide of the distribution of the roles or the schedule of their actions to be efficient. It has been proposed that leaders could bring benefit to the group by facilitating group organisation and coordination (Calvert, 1992).

Leader-follower as a solution to coordination problems appears already in dyadic interactions (King et al., 2009). Evolutionary game theory shows that most of coordination problems between two individuals can be solved by a single coordination game in which individual has to choose between the strategies lead or follow (for an example, see producer-scrounger models Barnard and Sibly 1981; Rands et al. 2003; Giraldeau and Livoreil 1998).

Johnstone and Manica (2011) proposed a model based on game theory to explore the emergence of leaders in a population faced to coordination problems. They define individuals by an intrinsic value of influence which determines the probability of an individual to choose their own preference or to copy the preference of another interacting individual. The individuals interact in repeated coordination game in which choosing the same strategy carry the largest output. Their results show that natural selection leads to stable dimorphism with the presence at equilibrium of individuals with low influence, i.e. followers and individual with high influence, i.e. leaders. These results are explained by the trait of leadership being advantageous when a majority of individuals are followers (and vice versa). This model successfully demonstrates how coordination costs can lead to the evolution of leadership because of the benefits it provides to individuals. However, these models do not consider the case where leaders get more resources than followers, which is the main limit of functional explanations of the emergence of leadership. In addition, they consider small group size (maximum of 10) at which humans can easily solve coordination games by communicating with each other.

Powers and Lehmann (2014) developed a theoretical model of evolution of leadership taking in account the additional benefit of being leader and high group size. Their results show that it is possible to obtain the evolution of stable preferences toward hierarchical organisation and thus the emergence of hierarchy. Importantly, this result holds in presence of inequality, i.e. with leaders receiving more resources than followers. The authors explain this result by a feedback loop between social organisation and group size. The average higher production in hierarchical groups leads to hierarchical group being bigger. In return, these groups can produce larger amount of resources by economy of scale [5]. However, these large groups also have more difficulties to organise. As follows, the advantage of having hierarchy in these large groups is higher. This feedback loop ultimately leads to the evolution of groups with stable hierarchy and high group size. These groups spread hierarchical organisation by sending a larger number of migrants to other groups. The authors also show (as seen in coercive theories) that leaders temper their level of despotism to prevent the departure of unsatisfied followers and then maintain a higher total production of resources on which the leader will take a share. The work of Powers and Lehmann (2014) shows that the emergence of hierarchy can be explained by the facilitating role of leaders on group organisation. In particular, they shed light on how the demographic increase can interact with the evolution of hierarchy. In addition, their results on the level of inequality confirm results of coercive theories and show that both processes are compatible. However, this model applies to institutional hierarchy but does not explain how leadership would have evolved before the advent of institution such as voting systems.

2.2.2.4 Functional theories: summary

Functional theories state that hierarchy is the result of benefits brought by leaders. Because leaders reduce defection in the group and help organise large-scale cooperation, followers voluntarily choose hierarchical groups even at the cost of relative domination. As we have seen, models identify the size of the group as a main factor. Indeed, an increase in the size of the group lead to the failure of small-scale mechanisms to maintain cooperation (Powers and Lehmann, 2017) and an exponential increase in the cost of organisation (Johnson, 1982). Functional theories underly a major mechanism which successfully encompasses one facet of hierarchy. However, functional models fail to explain the evolution of high level of despotism as seen in archaeological record. In addition, the arguments advanced to explain the spread of functional hierarchy are struggling to explain the emergence of hierarchy only from the evolution of individuals and in absence of political institutions.

2.3 The iron law of oligarchy

On the one hand, coercive theories successfully explain the emergence of despotism in which dominant leaders exploit submitted followers. They identify an important equilibrium between capacity to impose domination and capacity to avoid it, and how environmental factors can affect these. However, coercive theories fail to explain

[5] Economy of scale describes the fact that an increase in the scale of an operation (here group size) is translated into a superlinear increase in the benefit produced by the operation Pindyck and Rubinfeld, 2001

how leaders have developed dominance in the first place and overlook the extensive evidence of leaders' beneficial roles in the group. On the other hand, functional theories successfully explain the evolution of mutualistic leaders and their acceptance by followers. They identify major mechanisms such as the role of leaders in monitoring defectors and facilitating group coordination. However, functional theories rely on particular conditions and overlook the development of despotic behaviours. In truth, both sides agree on a multi variant explanation of the evolution of hierarchy. Rather than ignoring the other side, coercive and functional theories appear to be looking at different properties of leaders. Coercive theories focus on inequality in term of resources. Functional theories focus on inequality of power, which leaders use to benefit the group. However, there are only few models which encompass the evolution of both inequality (Powers and Lehmann, 2014; Hooper et al., 2010; Hooper et al., 2015). Nonetheless, inequality of power and resources could be strongly connected. For instance, power over others' behaviour or collective decision could be an efficient way for a leader to build up economic advantage.

To find such theory, we now temporarily walk away from the evolutionary biology literature to take a glimpse in the large amount of research conducted by sociologists and political scientists. These fields have for long try to understand the mechanisms and processes underlying the distribution of power. One particular theory seems to fulfil the previous gap by proposing the emergence of hierarchy and despotism from a same property, inequality of influence (Michels, 1911). We now present this theory and draw the parallel between it and previous theories studied in evolutionary sciences.

The "iron law of oligarchy" is a theory from political sciences, which has been proposed a century ago by Robert Michels (Michels, 1911). Building on his disappointing experiences as member of a political party in the early 20th, Michels proposes that any human organisations, however democratically committed they can be, will inevitably fall into an oligarchic organisation [6] (Michels, 1911). In other words, human groups are bound by an iron law to end up as an oligarchy. More interestingly for this thesis is the process that Michels proposes to explain how groups would switch from egalitarian to oligarchy. First, he states that large-scale groups are constrained by high costs of organisation and thus require to entrust the decision-making to a minority of individuals if they want to function efficiently. In order to facilitate decision-making, this minority will be given power and authority over other individuals. Once few individuals have a large power over group decisions, it is in their interest to use this power to maintain and develop their domination. This minority of individual will then do whatever it is necessary to maintain their position and block any opposition, ultimately overpassing democracy. At the end, the group is an oligarchy, in which the structure of power is an end in itself rather than a mean.

[6] Oligarchy is here defined as a concentration of illegitimate power in the hands of an entrenched minority (Leach, 2005).

This theory has been built upon a large set of evidence and is still nowadays a recognised theory in political sciences (for a short review, see Leach 2015; Tolbert 2010). How does this theory fits with evolutionary theories of hierarchy? It draws interesting parallels but it also adds important subtleties. As functional theories, the iron law of oligarchy states that leaders emerge to reduce the cost of organisation. Nonetheless, it narrows the role of leaders to collective decision-making, which would be facilitated by the concentration of power into few individuals. As coercive theories, the iron law of oligarchy states that once an individual has build up dominance, this individual will use it to strengthen its position and exploit others. Nonetheless, it proposes that an excess of political power, i.e. power over collective decisions, is enough for leaders to impose their domination, rather than a fighting or economic advantage. Crucially, the iron law of oligarchy combines coercive and functional theories and explain the emergence of hierarchy and despotism. It proposes that both sides emerge from a same inequality: inequality of influence.

Nonetheless, the iron law of oligarchy also has been the target of a number of criticisms. In particular, new evidence on other human organisation rose concerns on the generality of this law. The main criticisms denote three parts of the iron law which lack of explanation:

- Why do large-scale organisations need to centralise power in order to be effective (Breines, 1980; Rothschild and Whitt, 1986)? Some organisations, e.g. cooperative and worker's collectives, have exhibited egalitarian and democratic organisation.

- How does the political power owned by leaders provide them with a mean to exploit others? Marxist scholars claim that leaders require economic power and control of the means of production rather than political power (Bukharin, 1925; Hook and Hook, 1933),

- Why would leaders necessarily become despotic (Edelstein, 1967; Schumpeter, 1942)? First, it is not clear what is the force driving leaders to dominate others. Second, there have been example of groups where despotism is limited because the minority is still accountable to majority [7].

These criticisms have shown that the iron law of oligarchy might not apply to all human groups, or at least that the iron law applies in more particular conditions than the ones initially stated. These criticisms have been hard to answer because the iron law of oligarchy lacks of a more formal description. As a result, most of criticisms are new evidence contradicting the predictions of the iron law of oligarchy, rather than criticisms on the law itself, i.e. the causal links it proposes. It is then hard to see if the law needs to be totally rejected or if some parts of the law need to be refined. In particular,

[7] This critic is based on examples of groups in modern human societies but it draws an interesting parallel with the egalitarian norms observed in tribes of hunter-gatherers

the iron law of oligarchy describes the change in individuals and societies with time, but yet lacks of a formal description of how individuals change. For instance, it is hard to answer why would leaders develop despotic behaviours if we do not consider the rules by which leaders' behaviours change with time.

In this thesis, we argue that an evolutionary point of view can answer these criticisms or at least provide means to investigate them. This is because evolution provides a precise and formal description of a missing mechanism, how individuals change with time. The theories that we have presented earlier already answer some of the gaps of the iron law of oligarchy. For instance, the question of "why would leaders develop despotic behaviours" is easy to answer when looking at it through the lens of natural selection. Coercive theories show that despotism provides an evolutionary benefit to leaders because leaders get a higher amount of resources and so a higher amount of offspring. With time, the numerous offspring of despotic leaders will replace the fewer offspring of a more tempered leader. In addition, reproductive skew theory clearly identifies the effects of different factors on this level of despotism. Another gap of the iron law of oligarchy is to explain "why would a bigger group necessarily lead to the concentration of power in a minority". If we consider that leaders facilitate group organisation, functional theories show that hierarchy will evolve because followers present in a group with leader will exhibit a higher fitness than followers in other groups. Ultimately, it creates a selection pressure toward hierarchy. Yet, this explanation does not solve totally the problem because this selection pressure can be counterbalanced by the competition between individuals of the same group, which pushes every individual to become leader. However, the evolutionary point of view narrows down the problem to a measurable and well known problem in evolutionary biology (Frank, 1998).

In its recent review of the iron law of oligarchy, Leach (2015) states that: *"Despite over a century of empirical research in a range of subfields in political science and sociology, however, there is still no consensus about whether or under what conditions Michels' claim holds true"*. Evolution theory is able to fill this gap because it describes precisely the relation between environmental factors and changes in human behaviours. The approach of evolutionary dynamics reinterprets problems in term of cost and benefit to measure in which direction selection forces drive change. The mechanistic approach of this framework, combined to its mathematical description provides the mean to create precise predictions, which would describe under which conditions the iron law of oligarchy will hold. In return, the iron law of oligarchy provides a new hypothesis strongly supported by evidence for the field of evolution of hierarchy.

Thus, we propose in this thesis an evolutionary iron law of oligarchy. The evolutionary iron law of oligarchy proposes a formal model of the iron law of oligarchy, based on a well-accepted body of theory. Following the iron law of oligarchy, we define hierarchy by the distribution of individual capacity to influence collective decision. The evolutionary iron law of oligarchy describes the evolution of this trait, influence, and explain how it creates inequality of power and resources. The scenario proposed by the theory is that an increase in group size leads to a skewed distribution of influence. This is because a skewed distribution of influence facilitates collective decision-making and thus, increases the reproductive success of the members of the groups. Once in place, influential leaders evolve despotic behaviour and create economic inequality. This is because they can use their influence to bias the collective decisions and increase their reproductive success. They bypass the watch of egalitarian members of the group by biasing their opinions. This scenario is testable using an evolutionary dynamics framework, which describes the different selection forces and how they are affected by the environmental factors. We propose in this thesis to build models which represent this scenario and investigate if this scenario holds.

However, there is still one process lacking of a formal description. The iron law of oligarchy proposes that the benefit of leaders emerge from collective decision-making. But how to model collective decision-making and in particular the effect of the distribution of influence on it? Fortunately, such dynamics have been studied by a different field. Statistical physics have developed models which describe how individuals reach consensus. We argue that these models might provide the last missing block to create models of the evolutionary iron law of oligarchy.

2.4 Modelling consensus decision-making with opinion formation models

The social dynamics of groups have been studied by the field of statistical physics using opinion formation models. Opinion formation models are theoretical models, which combine physics and mathematics tools to social and psychological evidence. Although the concerned literature do not explicitly talk about leadership, we propose that opinion formation models actually provide crucial insight in the role of leaders in group organisation.

Opinion formation models describe a population of individuals by their opinions, the capacity of individuals to transmit their opinions and the possible interactions. At each time step, the model simulates update events during which, one individual shares its opinion to other individuals. The listeners then modify their opinions according to the opinion of the speaker, modulated by some characteristics of the speaker and themselves. Opinion formation models usually focus on the possibility to reach a consensus, on the time to reach it and the final decision as a function of the network structure. One of the first and perhaps most studied discrete opinion formation model is the *voter model* (Clifford and Sudbury, 1973; Holley and Liggett, 1975). Here, individuals are characterised by a binary state variable and, on each time step, a randomly chosen individual adopts, or "copies", the state of one of its neighbours. Worth citing is also the

Deffuant model, which extends voter model to continuous opinions (Deffuant et al., 2000).

Opinion formation models provide a mechanistic description of collective decision-making. Hierarchy can be integrated in these models by considering that individuals can differ in their capacity to transmit their opinions. Studying the effect of hierarchy on collective decision-making is then studying the effect of heterogeneity of individual characteristics on collective decision-making. That is why if the extensive literature on opinion formation models have been reviewed (Baxter et al., 2008; Baxter et al., 2012; Blythe, 2010), we will focus now on the study of heterogeneous opinion formation models.

First, heterogeneity can be integrated by considering that some individuals are stubborn and do not want to change their opinions. Masuda et al. (2010) develop the partisan voter model in which each individual has an innate and fixed preference for one of two possible opinion states. They show that the presence of these individuals slow down the time to reach consensus. Mobilia (2003); Mobilia et al. (2007) introduced a voter model with "zealots", i.e. individuals that always maintain its opinion. Their results indicate that the presence of a zealot can strongly bias the final average opinion. Their model also shows that zealots can have a negative effect by potentially preventing the group to reach consensus. Galam and Jacobs (2007) found similar result in an opinion formation model where individuals update their opinions as a function of the local majority. To summarise, the presence of stubborn individuals appears to bias the overall opinion and to slow down the consensus.

On the other hand, Sood et al. (2008) show that heterogeneity can be beneficial. They generalise emblematic opinion formation models - voter models and invasion process - to heterogeneous networks. They found that consensus is reached faster when the degree distribution is broad and that some individuals have a high number of neighbour. Pérez-Llanos et al. (2018) studied an opinion formation model in which individuals differ in their capacities of persuasion and zealotry (opposite of stubbornness). They show using an analytical approach that the time to reach consensus can be reduced by having a number of stubborn agents. Gavrilets et al. (2016) have developed an opinion formation where they investigate the effect of persuasiveness, stubborness and talkativeness (represented by reputation) on the time to consensus. Leaders can then be described as individuals with high stubbornness and high persuasiveness and followers as the opposite. The main results of their model demonstrate that the time to consensus is highly dependant of the heterogeneity in stubbornness and persuasiveness of individuals, e.g. the presence of few stubborn individuals can strongly slow down the consensus. Interestingly, they show that a high diversity of stubborness, persuasiveness and talkativeness can lead to very short or long time to reach consensus. They suggest that the shortest time appears when there is a minority of leaders and a majority of followers. However, they have a limited exploration of the effect of leaders and followers on this time to consensus because they look at the effect of the diversity (range of possible values) rather than the effect of distribution of these characteristics. Finally, Jalili (2013) developed a continuous opinion formation where individuals are characterised by a social power. Social power is equivalent to the capacity of an individual to change someone else opinion, i.e. persuasion. Importantly, they do not consider that consensus has to be reached but rather measure the size of the biggest group who reached consensus. Using this model, Jalili (2013) showed that when social power is asymmetrically distributed and concentrated in the individual with the highest number of social connection, the consensus is improved with the largest cluster at the end of consensus moving from 30 to 85%. Importantly, it does not work on other network structure in which there is not large differences in number of social links. Thus, it suggests that talkativeness is as important as persuasiveness.

Overall, these opinion formation models demonstrate that heterogeneity in opinion formation models can have different effects. First, the presence of stubborn, talkative and persuasive individuals bias the collective decisions. Second, it can slow down or speed up the time a group spend to reach consensus. However, general conclusion on the effects of different distributions of these characteristics on the time to consensus is still lacking. In addition, the presence of different characteristics and the hidden effect of network structure (network structure can affect the interactions possible but also the probability of speaking) limits comparison between the models.

To summarise, theories on the evolution of social hierarchy either successfully explain the despotic or mutualistic side of hierarchy. Although they recognised the importance of both sides, for instance organisation to explain the first emergence of leaders or coercion to shift to despotism, they struggle to integrate them in a comprehensive model. The iron law of oligarchy proposes a scenario which unifies both functional and coercive theory but yet, this theory lacks of a formal investigation. Thus, we propose an evolutionary iron law of oligarchy, which reinterprets the previous theory with an evolutionary perspective. To do so, we combine models of social dynamics and evolutionary dynamics. On the one hand, opinion formation models describe the decision-making process and the effect of the distribution of influence on it. On the other hand, evolutionary models describes how the traits affecting influence would change with time. Using these models, we aim to show if an evolutionary iron law of oligarchy is a viable scenario to explain the emergence of hierarchy and despotism, and under which conditions this scenario would hold.

Third Chapter

The effects of hierarchy on collective decision-making

One of the core postulate of "the iron law of oligarchy" is that hierarchy facilitates group organisation. Yet, it lacks a mechanistic model describing how the presence of leaders and followers could provide this organisational benefit. We propose that leaders could reduce costs of organisation by reducing the time a group spend to reach consensus (consensus time in short). The consensus time is costly because groups that take too long to reach a decision may lose resources or eventually fail the collective task, e.g. no decision taken before a battle starts. In this chapter, we model collective decision-making to investigate the effect of the distribution of influence on the time a group spend to reach consensus.

3.1 Contribution

In this Chapter 3, we demonstrate that skewness in the distribution of influence is enough to reduce the consensus time and scalar stress, i.e. the increase of consensus time as group size increases. In addition, our results show that hierarchy with an influential single leader leads to bigger reduction in (i) the consensus time, (ii) the variation in the consensus time, and (iii) the increase in consensus time as group size increases.

3.2 Publications

A part of the work in this chapter has been published as:

- Cedric Perret, Simon T.Powers and Emma Hart, *Emergence of hierarchy from the evolution of individual influence in an agent-based model*, Proceedings of Artificial Life Conference 2017, MIT Press, 2017

- Cedric Perret, Emma Hart and Simon T.Powers *Being a leader or being the leader: The evolution of institutionalised hierarchy*, Proceedings of Artificial Life Conference 2019, MIT Press, 2019

In addition, a part of the work presented in this chapter has been submitted as:

- Cedric Perret, Emma Hart and Simon T.Powers, *Disorganised equality or efficient despotism: How group size drives the evolution of hierarchy in human societies*, Proceedings of Royal Society B: Biological sciences. Submitted in 2019.

3.3 Introduction

Leaders appear to play an important role in organising collective task whether it is collective hunting (Alvard and Gillespie, 2004) or state management. Unlike hunter-gatherer leaders who temporarily lead in situations in which they are knowledgeable, leaders of post-Neolithic hierarchies are permanent and take decisions about a wide range of topics. It suggests that leaders play a role in organisation beside their knowledge, a suggestion that is supported by leaders effectiveness and emergence being correlated with intrinsic capacities to “lead”, e.g. talkativeness, charisma (Judge et al., 2002). However, it is still not clear how leaders provide such benefit. For instance, leaders could facilitate inter-individual communication, control defectors (Hooper et al., 2010), or inspire followers (Bass, 1990).

One of the main candidate to explain the organisational benefit provided by leaders is that leaders could facilitate coordination (Calvert, 1992). To realise a collective action, individuals need to choose their actions in regard to other individuals’ actions (Cooper, 1999). For instance, to hunt a large game collectively, individuals need to choose their roles, their positions, their future movements and adapt all of these as a function of the reactions of the animal.

The difficulty of coordination problems is that an individual needs to find what other individuals are doing, in order to adapt their own actions. In addition, other individuals would do the same reasoning and potentially update their behaviours at the same time. When the task tackled is sufficiently common and repeated, coordination problems can be solved by cultural evolution, by which the best strategy becomes more common because it is more transmitted than others (Boyd and Richerson, 1985). However, individuals can not rely on cultural evolution when the task is novel or if the characteristics of the coordination problem change often. In these cases, individuals can learn the optimal strategy by trial and error (Lewis, 1969; Schelling, 1960). This can carry large costs because it requires many mistakes, in particular in large groups. Thus, study on the role of leaders in coordination problems have often been focused on the capacity of leaders to take the right decision, to make the group take the right decision or to enforce the decision taken (Calvert, 1992). However, it is unlikely that the cost of coordination in humans lies in the mistakes done during the learning process. Humans are able to bypass the trial and error process by communicating with each other to find the optimal strategy. It suggests that the cost of coordination lies in the time spent in communicating and agreeing on a collective strategy. The presence of stubborn individuals or partisans of one strategy can stretch the time the group spend to reach consensus (Mobilia et al., 2007; Galam and Jacobs, 2007). Although this consensus time is negligible in small groups, it can become fairly consequent in large groups because of the number of individuals which needs to coordinate and because of the increasing probability of the presence of stubborn individuals (Gavrilets et al., 2016). This time spent to agree on a common decision is costly because the time itself carries a cost, e.g. resources get depleted, or because time constraints can force individuals to take a sub-optimal decision, e.g. a quick decision has to be taken during battle. In the worst case, the collective task can be abandoned for example, when individuals have an outside option such as in a stag-hunt game (Skyrms, 2003).

Psychological evidence suggests that leaders are skilled communicators and could use these skills to quickly lead the group to a consensus. For instance, experiments show that verbal communication (Mullen et al., 1989) or extraversion (Judge et al., 2002) are consistent predictors of leadership emergence. Although collective decision-making has been widely studied (for review, see Castellano et al. 2009), there is limited work exploring the relation between individuals' capacities to communicate and consensus time. Notably, Gavrilets et al. (2016) have developed a model simulating collective decision-making where they investigate the effect of persuasiveness, stubborness and talkativeness (represented by reputation) on the consensus time. They show that heterogeneity can impact the consensus time and for instance, a high diversity of stubborness, persuasiveness and talkativeness can lead to very short or long consensus time. However, the model provides a limited exploration of the effect of leaders and followers on this consensus time because it looks at the effect of the diversity (range of possible values) rather than the effect of distribution of these communication skills.

We extend the model of Gavrilets et al. (2016) to investigate more deeply the role of influence in collective decision-making. Following previous works (Gavrilets et al., 2016) and psychology experiments (Judge et al., 2002), we incorporate three traits: persuasiveness, stubborness and talktativeness under one trait, influence. We do so because we are interested in measuring the effect of leaders on consensus time rather than the effect of each trait. These three traits are correlated and observed in leader profiles. For instance, psychology experiments suggest that both the quantity (talkativeness) and quality (persuasiveness) of communication are important to identify the leaders (Jones and Kelly, 2007). Using this definition of influence, we aim to answer the following question:

Research question. *Does a skewed distribution of influence within a group reduce the time to reach consensus?*

3.4 Model definition

We developed an opinion formation model based on previous work (Deffuant et al., 2000; Gavrilets et al., 2016). It is a model which consists of a sequence of discussions between individuals until their opinions are close enough, i.e. the group has reached a global consensus. Opinion formation models are well-known tools to study social dynamics (Castellano et al., 2009).

Individuals are described by an opinion x, which is a continuous value defined between $[0,1]$. The opinion x describes a generic opinion of an individual on how to realise a collective task, e.g. next raid target, plan of an irrigation system or value of a law. Each time step is defined by one discussion event during which one individual, the speaker, talks to multiple individuals, the listeners. The individuals repeat the previous step until consensus is reached, i.e. the standard deviation of the opinions is less than a threshold. The number of discussion events that occurred to reach consensus is called the consensus time.

The novelty of the model is to explicitly describe individual capacity to influence the collective decision α (in short influence), which is a continuous value defined between $[0,1]$. The trait α represents the influence of an individual and affects (i) the capacity of one individual to modify the opinion of another individual towards its own opinion, (ii) the reluctance of an individual to change its opinion, and (iii) the probability that an individual talks to other individuals. These three traits, i.e. persuasiveness, stubbornness and talkativeness, are highly correlated in leaders personalities (Judge et al., 2002) and are the key factors in explaining how leaders reduce consensus time (Gavrilets et al., 2016). Influence represents a set of behavioural traits that affect the influence of an individual, such as extraversion, boldness, and charisma. To study the effect of social organisation on collective decision-making, we divide individuals into two profiles: leader L, and follower F. Each profile has a fixed value of influence α such that $\alpha_{\mathrm{L}} > \alpha_{\mathrm{F}}$.

We consider a population of N individuals. At the beginning of the opinion formation model, the values of opinion x are sampled from the uniform distribution between $[0,1]$. Doing so, we consider that individuals strongly differ in which decision should be taken. This scenario applies either when (i) the interests of individuals do not align or when (ii) the optimal decision is not known (or not trivial to guess). If both of these conditions are not fulfilled, it is likely that the group would reach a quick consensus, and thus time to reach consensus is negligible. The generality and limits of this assumption is presented later in the discussion section.

Each time step is defined by one discussion event during which one individual, i.e. the speaker, talks to multiple individuals, i.e. listeners. The probability P of an individual i to be chosen as a speaker s is an increasing function of its α value as follows:

$$P_i(t) = \frac{(\alpha_i(t))^k}{\sum_{n=1}^{N}(\alpha_n(t))^k}. \tag{3.1}$$

The exponent k defines how much the difference in influence is translated into a difference in the probability to talk. In the simulations we chose $k = 4$ so that in a group of 1000 individuals with the most extreme hierarchy, the probability that a leader is chosen as a speaker is very high (close to 90%). Indeed, we want to explore the whole scope of social organisation which ranges from everybody having the same probability to speak to one individual with an extremely high probability to speak. The speaker talks with N_{l} listeners randomly sampled from the other individuals in the group. This limit on the number of listeners models time constraints, and cognitive constraints of human brains (Dunbar, 1992).

We assume that every individual can be chosen as a listener, i.e. the social network is a complete network, in order to avoid explicitly modelling the network structure, and hence to keep the model tractable. This assumption is conservative because a more limited social network structure should only restrain more the interactions and thus should increase the consensus time. We also consider that individuals interactions are not limited to individuals with close opinions (as in models with bounded confidence Deffuant et al. 2000) because this model describes a consensus decision-making process where individuals are willing to convince each other. During a discussion event, a listener v updates its preference to a value x'_{v} following the equation below, where v represents the listener and u the speaker:

$$x'_{\mathrm{v}} = x_{\mathrm{v}} + (\alpha_{\mathrm{u}} - \alpha_{\mathrm{v}})(x_{\mathrm{u}} - x_{\mathrm{v}}). \tag{3.2}$$

We assume that the position of speaker gives a slight influential advantage over the listeners. Therefore, the minimum difference of influence $\alpha_{\mathrm{u}} - \alpha_{\mathrm{v}}$ is set to a positive low value, here 0.01. This assumption is necessary to avoid a systematic convergence of the opinions towards the individual with the highest α, a phenomenon not observed in real life. The individuals repeat the previous step until consensus is reached, i.e. the standard deviation of the opinions is less than a threshold x_θ. The number of discussion events that occurred to reach consensus is called the consensus time, t^*. We considered only global consensus, i.e. all the group agree. However, the global consensus is more or less tolerant to deviant opinions as a function of the consensus threshold x_θ.

3.5 Results

Opinion formation models are commonly studied using analytical methods in which is calculated an exact solution. However, these approaches are difficult in presence of heterogeneity in the population as it is the case here with individuals having different values of influence. Thus, we implement the model as an individual-centred model and use numerical simulations to analyse it. We focus on the effect of the following parameters: (i) the level of hierarchy represented by the number of leaders and the difference of influence α between leader and follower profiles (in short difference of influence) and (ii) the size of the group. The influence of leaders α_{L} and the influence of follower α_{L} are set symmetrically around 0.5. For instance, a difference of influence of 0.5 means that $\alpha_{\mathrm{L}} = 0.5+0.5/2 = 0.75$ and $\alpha_{\mathrm{F}} = 0.5-0.5/2 = 0.25$. The default parameters are for the consensus threshold $x_\theta = 0.05$, the number of listeners $N_{\mathrm{l}} = 30$, group size $N = 500$, the influence of leaders $\alpha_{\mathrm{l}} = 0.75$ and the influence of followers $\alpha_{\mathrm{f}} = 0.25$. The results presented are the mean across 100 replicates for each set of parameters presented. The error bars or ribbon, when not described in the caption, represent the standard error from the mean. The error bars might not be visible when they are too small.

3.5.1 Hierarchy and consensus time

Figure 3.1 shows the main result: the presence of a minority of influential individuals and a majority of influenceable individuals reduces the time a group spend to reach consensus. This result is consistent across different values of influence α for leader and follower profiles. This result shows that a skewed distribution of influence is sufficient to explain the benefit of hierarchy on collective decision-making. Importantly, the differential quality of information that leaders might posses, and which might lead to a group with hierarchy making better decisions, is not required to get this result. When the difference in influence is low, the consensus time is the shortest when multiple

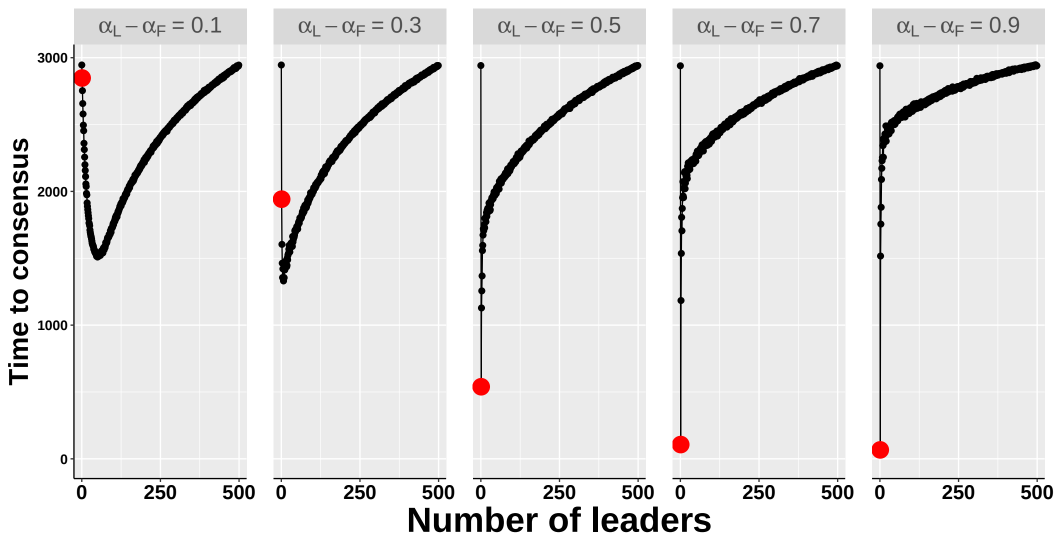

Figure 3.1: Consensus time as a function of numbers of leaders and the difference in influence between leader and follower profiles. The consensus time for single-leader hierarchy is shown in red. The results presented are the average across 100 replicates.

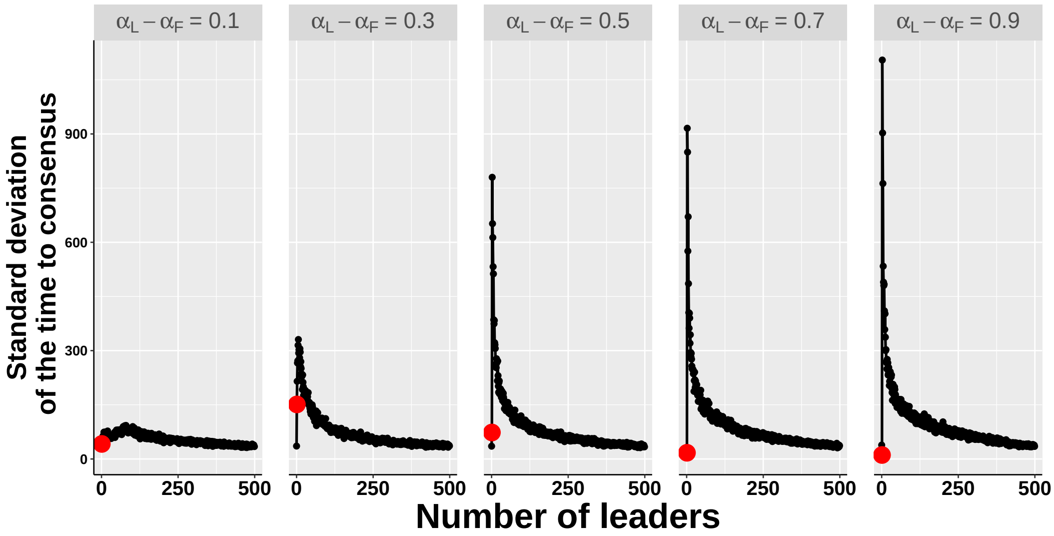

Figure 3.2: Standard deviation of the consensus time as a function of numbers of leaders and the difference in influence between leader and follower profiles. The standard deviation of the consensus time for a single-leader hierarchy is shown in red. The results presented are the average across 100 replicates.

influential leaders are present. For high difference in influence, hierarchy with single leader has the shortest consensus time. In other words, increasing the difference of influence leads to a slower consensus time for multiple leaders hierarchy but a shorter consensus time for single-leader hierarchy. Across different values of influence for leader and follower profiles, the shortest consensus time is obtained in presence of one single extremely influential leader and the rest of the group as influenceable followers.

Figure 3.2 provides a better insight in the effect of number of leaders on the consensus time. The result shows that when the consensus time for multiple leaders is high, e.g. high difference of influence, the standard deviation in the consensus time is also high. This shows that the consensus time is highly variable between replicates. This is because the consensus time in presence of multiple leaders is highly dependant of the opinions of these leaders, i.e. fast when opinions are close, and slow when opinions are more divergent. Groups with multiple leaders with high influence and different opinion are slow to reach consensus because multiple leaders (i) are slower to be convinced, (ii) can increase divergence by convincing followers towards extreme opinions and (iii) can convince followers from other leaders. On the other hand, Figure 3.2 shows that egalitarian group, i.e. homogeneous group, has a long consensus time but low variation in the consensus time. This result suggests that the long consensus time in egalitarian group is due to a slow convergence rather than conflict between leaders. Similarly, single-leader hierarchy always has a small standard deviation in the consensus time. It suggests that groups with a single leader with low influence spend more time to reach consensus simply because leader is less efficient at bringing the opinions of others toward its own. The fact that the leader is stubborn has no effect because he is the one convincing the rest of the group.

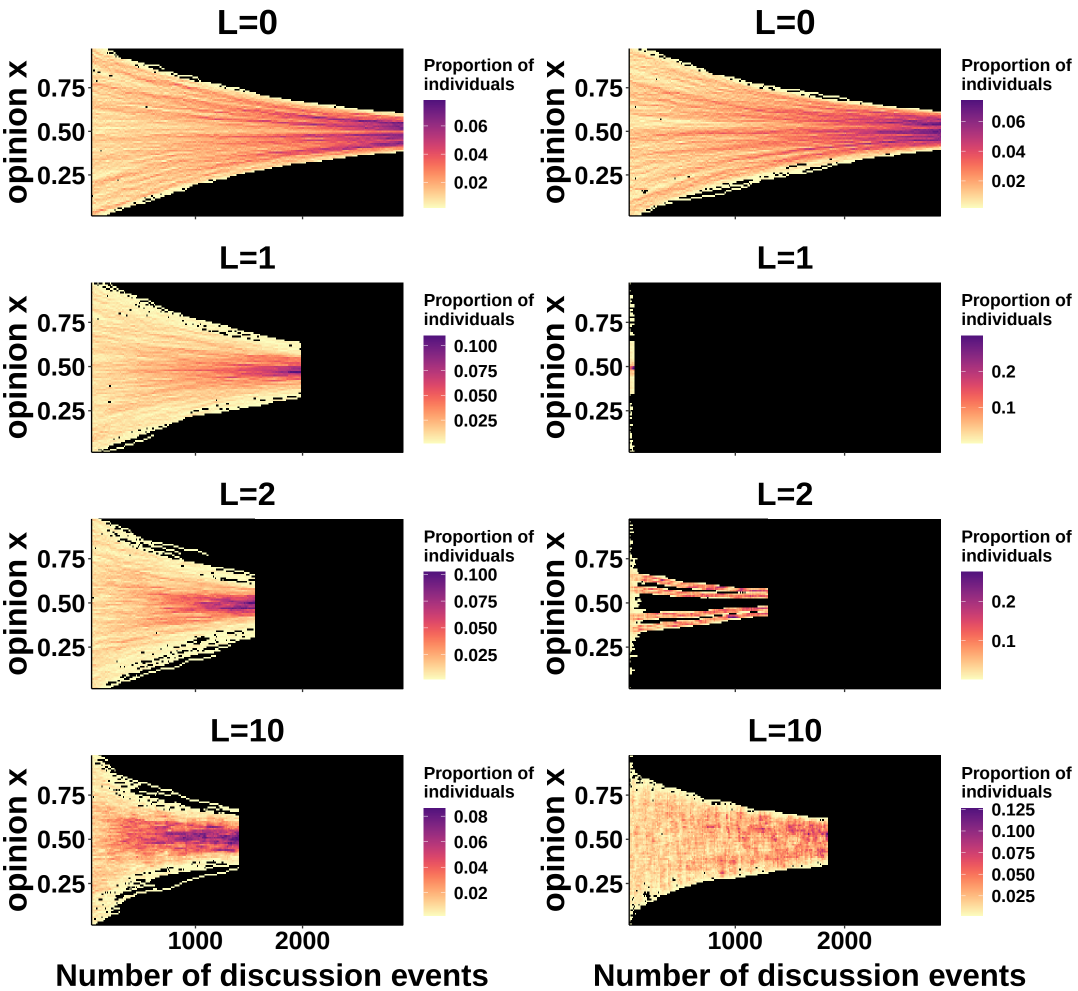

Figure 3.3: Density distribution of individual opinion as a function of number of discussion events for different number of leaders: from top to bottom $0, 1, 2, 10$. On the left, the difference of influence is small 0.3. On the right, the difference of influence is high 0.7. The background is set to black and it represents the absence of any individual with this value of opinion. For illustration, the difference between the initial opinions of leaders are set to be maximum and equidistant. The plot represents results for a single run.

Figure 3.3 illustrates the opinion formation process and the effect of the number of leaders on collective decision-making. When the difference of influence between leaders and followers is low (on the left), the pattern of convergence is not much affected by the number of leaders. This is because leaders and followers have close influence and thus, do not create strong variations. Multiple leaders are more efficient because leaders convinced each other and once their opinions are close, they quickly convince the rest of the group. When the difference of influence between leaders and followers is high (on the right), the pattern of convergence is much more affected by the number of leaders. First, we see that in the absence of leaders, or with a single leader, individuals' opinions slowly and consistently converge. The presence of a single leader speeds up this process as the leader quickly convinces the majority of the group. The presence of multiple leaders creates a more heterogeneous pattern of convergence. The presence of

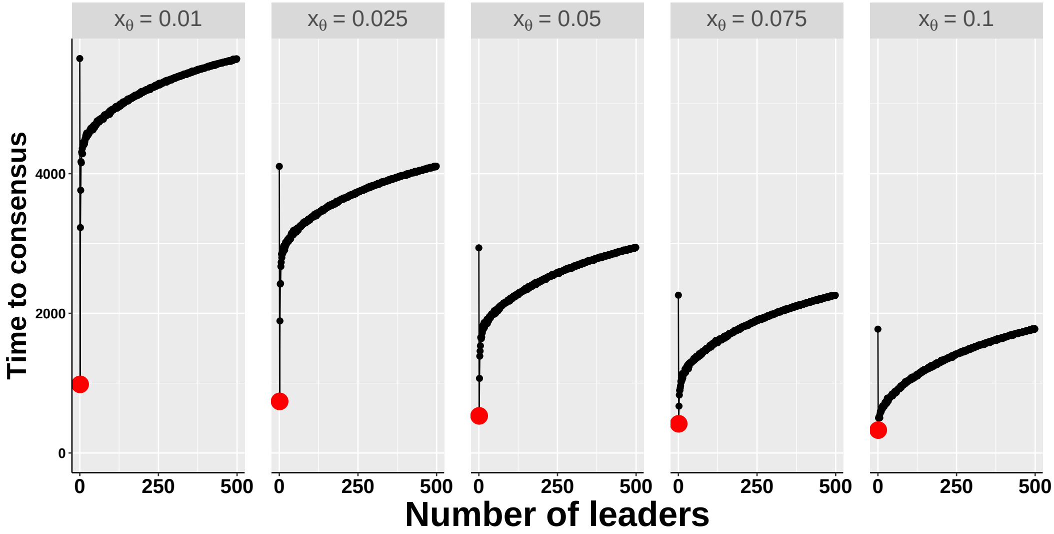

Figure 3.4: Consensus time as a function of numbers of leaders and different value of consensus threshold x_θ. The consensus time for single-leader hierarchy is shown in red. The results presented are the average across 100 replicates.

two leaders results into two cluster of opinions with the majority of followers switching from one leader to another: leaders alternatively convince individuals from the group but neither leader has enough followers to reach consensus. When more than two leaders are present, the majority of opinion fluctuates between the different leaders. In both cases, leaders' stubbornness slows down the convergence of leaders' opinions towards the others, which in turn slows down collective decision-making.

To summarise, hierarchy, i.e. a majority of influential individuals and a minority of influenceable individuals reduces the consensus time. When the difference in the influence between leaders and followers is low, multiple leaders has the shortest consensus time. When the difference in the influence between leaders and followers is high, single-leader hierarchy provides a benefit to group organisation because it has a shorter consensus time and a more constant consensus time. Overall, the shortest consensus time is reached for a hierarchy with a single influential leader.

We consider here that only global consensus is possible, i.e. the whole group agrees on the decision. We make this choice because we consider that all individuals need to participate to the task. We can vary the consensus threshold x_θ to allow for a more or less strict consensus, i.e. divergent opinions are more or less accepted.

Figure 3.4 shows that the main result is consistent across different value of consensus threshold x_θ: a minority of influential individual and a majority of influenceable individuals leads to shorter consensus time. On the one hand, the consensus time for single-leader hierarchy is only slightly affected by the consensus threshold. This is because in a single-leader hierarchy, the leader convinces each listener in one discussion and thus, the consensus time is simply the time for the leader to talk to all individuals. On the other hand, the consensus threshold strongly affects the consensus time for

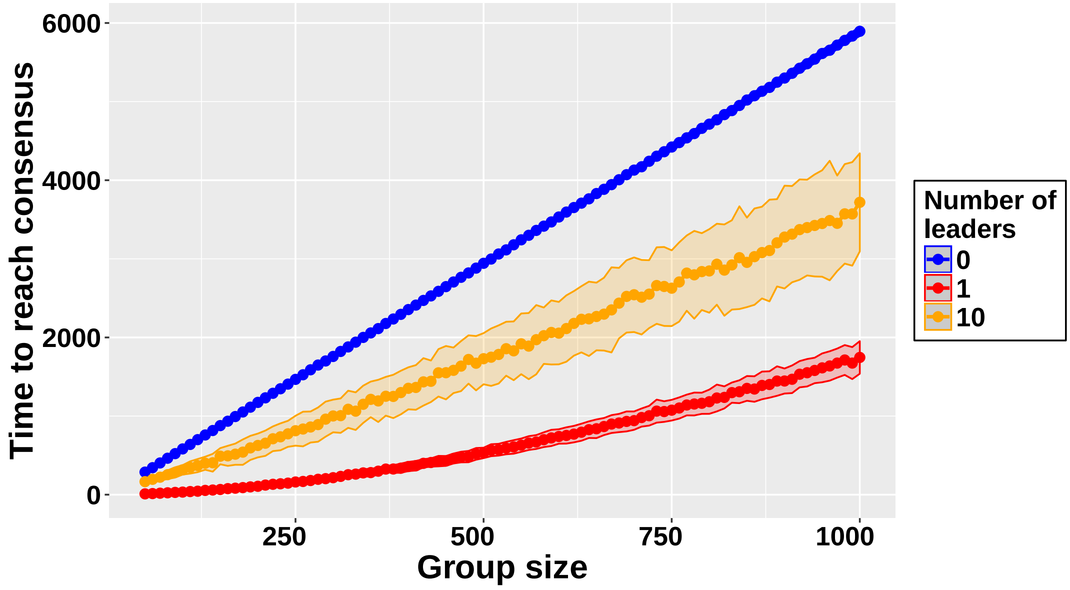

Figure 3.5: Consensus time as a function of the size of the group for three different types of social organisation: (i) 0 leaders, (ii) 1 leader and (iii) 10 leaders. The ribbons represents the standard deviation to highlight the high variance in the consensus time when multiple leaders are present. The results presented are the average across 100 replicates.

egalitarian and multiple leaders hierarchy. In the case of egalitarian, a higher consensus threshold reduces the consensus time because individuals can have more different opinions at consensus and thus, need to be convinced less. In the case of multiple leaders hierarchy, a higher consensus threshold reduces the consensus time because the group can ignore the diverging opinions of few stubborn leaders.

3.5.2 Hierarchy and scalar stress

The cost of consensus decision-making is considered particularly important in large groups and functional theories propose that the main role of leaders and hierarchy is to limit the increase of this cost with group size i.e. limits scalar stress (Johnson, 1982; Powers and Lehmann, 2014). Thus, we now investigate the effects of group size on the time to reach consensus and how hierarchy as we defined it, affects this relationship. The group sizes considered for the replicated simulations are from 50 to 1000 with an increment of 50. The number of leaders considered is only between $[0, 50]$ because they are the instances where a consensus time for each possible group size can be measured. For instance, there is only one case of a group with 1000 leaders.

Figure 3.5 presents the increase in consensus time for three different social organisations, an egalitarian group (no leaders), hierarchy with one leader, and hierarchy with ten leaders. Figure 3.5 shows that hierarchy reduces scalar stress, i.e. the gradient of consensus time with respect to group size is lower. Again, the differential quality of information that leaders might posses, and which might lead to a group with hierarchy making better decisions, is not required to get this result. The results also show that the

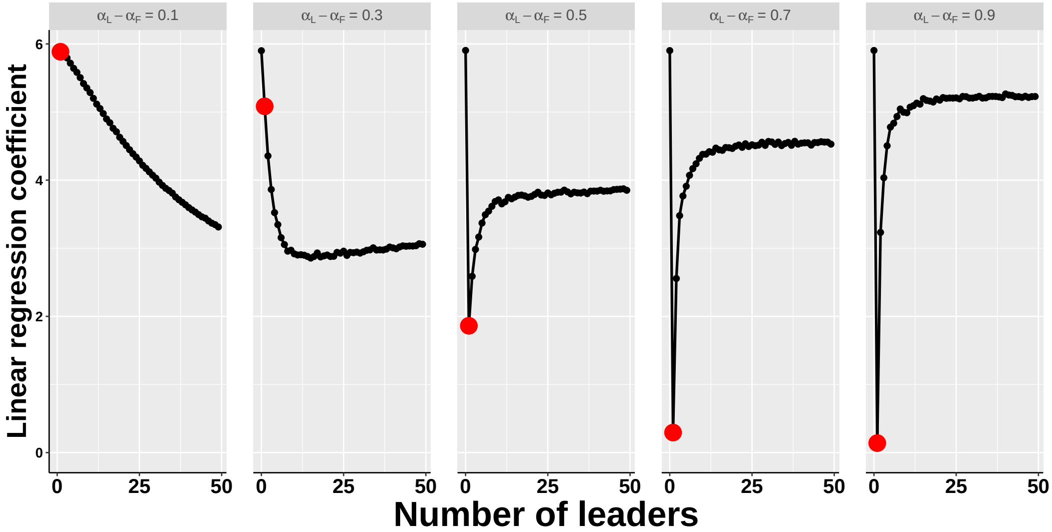

Figure 3.6: Scalar stress (represented by linear regression coefficient) as a function of numbers of leaders and the difference in influence between leader and follower profiles. The linear regression coefficient for single-leader hierarchy is shown in red. The results presented are the average across 100 replicates.

presence of multiple leaders reduces the benefit of hierarchy and increases the variance in the consensus time.

To provide a more thorough investigation of the effect of size on consensus time, we present the regression coefficient of the linear regression of consensus time on size. Note that the relation between consensus time and size is not perfectly linear for a small number of leaders and thus, the coefficient estimated is slightly off. However, the relation is close to linear and we are interested in clear differences rather than small quantitative differences. Figure 3.6 shows that scalar stress has similar behaviour than the consensus time. First, hierarchy has a lower scalar stress for any difference between the influence of leaders and followers. Second, multiple hierarchy has the lowest scalar stress when the difference is low and single-leader hierarchy has the lowest scalar stress when the difference is high. Third, the lowest scalar stress appears for groups with a single leader with high influence.

Figure 3.7 shows that the scalar stress is strongly dependant of the number of listeners N_{l}. It demonstrates that a lower number of listeners results in an increase in consensus time, in particular for egalitarian group and multiple leaders hierarchy. This is because a low number of listeners (i) slows down the overall convergence and (ii) slows down the convergence between groups of stubborn leaders and their convinced followers. For a high number of listeners N_{L}, the consensus time for multiple leaders hierarchy is close to the consensus time for single-leader hierarchy.

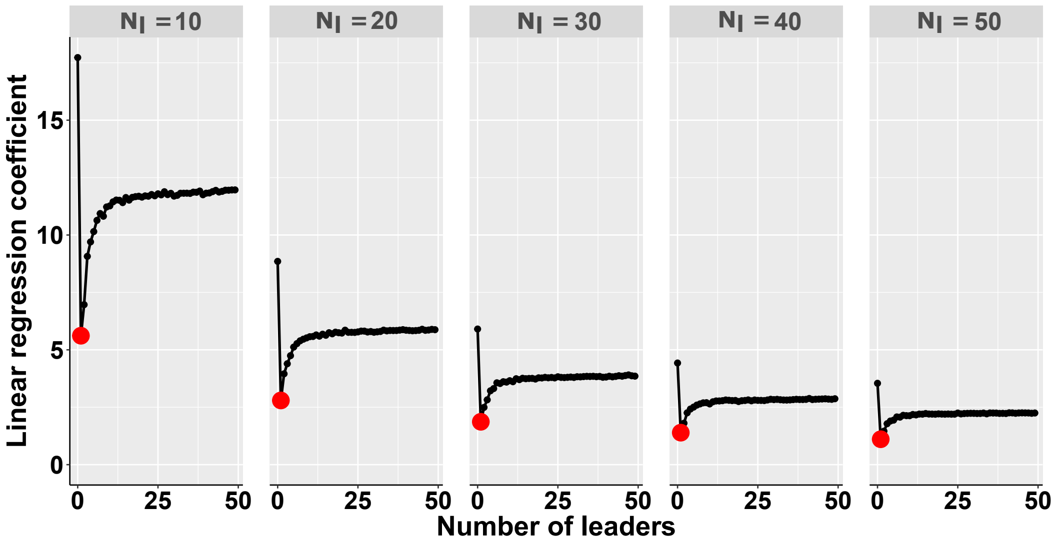

Figure 3.7: Scalar stress (represented by linear regression coefficient) as a function of numbers of leaders and number of listeners N_l.The linear regression coefficient for single-leader hierarchy is shown in red. The results presented are the average across 100 replicates.

3.6 Discussion

Ethnographic data suggest that leaders provide an important benefit to the group by reducing the cost of consensus decision-making (Carneiro, 1967). In particular, this benefit would be amplified in large groups i.e. leaders would reduce scalar stress (Johnson, 1982; Alberti, 2014). We investigate these effects in an opinion formation model which integrates heterogeneity in individuals' capacity to influence. We use numerical simulations to investigate the qualitative effect of number of leaders and group size on the consensus time. First, our results show that the presence of influential leaders and influenceable followers reduces the consensus time. Second, the presence of influential leaders and influenceable followers reduces scalar stress, i.e. the gradient of consensus time with respect to group size is lower. Importantly, both of these benefit emerge solely from the difference of influence between leaders and follower. Third, the highest and most constant benefit is obtained for a hierarchy with a single leader with extreme influence.

These results confirm the hypothesis that social hierarchy provides a benefit to group organisation and that this benefit increases as group grows (Calvert, 1992). Our results complete this hypothesis by showing that the difference in individual capacity to influence is sufficient to explain the organisational benefit of social hierarchy. In addition, the work presented here provides a mechanistic model of the role of hierarchy in collective decision-making that can be applied across a wide range of domains.

This work expands on previous research in social dynamics. A previous opinion formation model shows that the benefit of hierarchy on organisation can emerge from micro-level interactions between individuals (Gavrilets et al., 2016). Their results focused more on the effect of diversity and only suggest that leader being persuasive, stubborn and talkative can provide a strong reduction to the consensus time. Our findings confirm this result and provide a more thorough exploration. In addition, it broadens their conclusion by showing that this effect is dependant of the number of leaders and the difference of influence between leaders and followers. In particular, we show that multiple leaders can have a limited benefit, because leaders persuade each others' followers, creating conflicts of interest between a large proportion of the group. Unlike their work, our model considers the three traits stubbornness, persuasiveness and talkativeness as one. Combining their work and ours, further work could disambiguate the effects of these three characteristics on the consensus time and provide a better understanding of how does hierarchy facilitate collective decision-making.

This prior work also shows that an increase in the group size slows down the consensus, because it creates more stubborn individuals (Gavrilets et al., 2016). Yet this effect was limited. Our results add that group size can have a very significant effect on the consensus time, and that this effect can be tempered by the presence of influential leaders. Previous work (Gavrilets et al., 2016) does not find a strong effect of group size on the consensus time because they consider that multiple discussion events happen during one time step and thus, the consensus time is divided by the number of discussion events per time step. However, such an assumption considers that individuals are able to group themselves in an exact and non-overlapping number of groups, e.g. 100 individuals getting split in 10 subgroups of 10 individuals. This process is unlikely in the absence of advanced institutions or rules stating how the division needs to be done. However, it fits well with more advanced forms of hierarchy such as states.

We considered here that the initial opinions widely differ between individuals. If the opinions were initially similar, the consensus would be reached quickly and leaders would provide a negligible benefit. So to which scenario this assumption of divergent opinions would apply? And *a fortiori*, in which collective tasks leaders could be expected to provide a significant benefit? First, this assumption would hold for tasks in which the interests of individuals do not align. This encompasses a large range of scenario as collective tasks often carry different benefits and costs for individuals. For instance, even if all individuals want to hunt, some would prefer to hunt at a different time, or have a different role, or get a higher share of the game. Yet, the benefit provided by leaders could vary as a function of the magnitude of the conflict of interests. This relationship could be explored by extending the presented analysis and considering different initial distributions of opinions. Second, the assumption of different initial opinions holds for coordination problems that are novels or changing enough for cultural selection to not solve the coordination problem. If the task is sufficiently repeated and its features remain sufficiently constant, cultural selection would favour the optimal decision and the opinions of individuals would converge toward a similar strategy (Boyd and Richerson, 1985). A good example of this scenario is the design of institutional rules (Ostrom, 1990) because the efficiency of institutional rules depends of the social environment and social environment often changes more rapidly than abiotic environment. For instance, the efficiency of a rule to enforce cooperation depends of the proportion of defectors, which itself depends of the efficiency of the rule (Dong et al., 2019). The relationship between the nature of the task and the benefit provided by leaders could be explored in the future by considering explicitly a task and integrating the cultural evolution of opinions.

We considered here a complete network and only global consensus, i.e. all the group agree. Despite both being conservative assumptions, they are two unlikely features of real world situations. Jalili (2013) developed an opinion formation considering local consensus where he looks at the effect of the distribution of persuasion (called social power) within different network structures. This model shows that when persuasion is asymmetrically distributed with the most connected individuals having the highest social power, the consensus is largely improved with the largest cluster at the end of consensus moving from 30 to 85 % of the total. Yet, this result does not hold on other network structures in which there is not large differences in the number of social links. Further work could integrate network structure to investigate the effect of hierarchy and group size as defined here on the consensus time. However, this requires a good representation of the social structure of individuals during consensus decision-making, which can be more dynamic than the social network observed in long-term interactions.

We have used numerical simulations to investigate the effect of leaders on consensus decision-making. An important next step is to investigate this question analytically and in particular, to get a mathematical description of the relationship between skewness of the distribution of influence and consensus time. Along this line, it is important to note the parallel between opinion formation models and population genetics models (Crow and Kimura, 1970). Indeed, the process of consensus-decision making as modelled here is similar to the fixation of alleles in a population only subject to random drift. It has been shown in population genetics that a high variance in reproductive success results in a stronger random drift and a faster fixation of allele (Wright, 1938). This result is close to our result of consensus being faster to obtained when individuals vary in their capacity to transmit their opinions. Pushing further, such analytical model would allow, by their simplicity, to explore more complex consensus decision-making process. For instance, if we consider that better ideas are more propagated, population genetics suggests that heterogeneity could be detrimental because it reduces the change that this opinion is chosen (more exactly, population genetics shows that heterogeneity in reproductive success increases the effect of random drift compared to selection). Yet, this parallel between the presented model and population genetics needs to be carefully examined to know how much results from population genetics could directly apply to the present case. Nonetheless, it is one of the most promising path to build an analytical version of this model and should be explored in further work.

Our results show one possible explanation for the benefit that leaders provide to group organisation but multiple mechanisms are likely to be involved. In particular, although Neolithic leaders might not have a more advanced knowledge or expertise than other members of the group (because they take decisions on a wide range of topics), they might be able to take better decisions by aggregating knowledge from different individuals. Yet, it is worth noting that such mechanism will be more important in multi-level hierarchy where lower-level leaders could report to higher-level leaders. Further work exploring this role of leader in decision-making could provide important insights on the evolution of bureaucratic states.

We have shown that differential influence is enough to explain the benefit of hierarchy. It has been hypothesised that this benefit could lead to the evolution of influential leaders and influenceable followers. Yet, there is a conflict between this group benefit and the individual cost of being a follower. In the next chapter, we investigate if this organisational benefit coupled to the demographic increase of the Neolithic transition can drive the evolution of leader and follower behaviours.

Fourth Chapter

The evolution of informal hierarchy

In Chapter 3, we have shown that the presence of a minority of influential and a majority of influenceable individuals facilitate group organisation because (i) it reduces the time a group spent to reach consensus and (ii) it reduces scalar stress, i.e. the gradient of time to consensus with respect to group size is lower. In this chapter, we investigate if this organisational benefit can lead to the evolution of leaders and followers behaviours and in such proportion, i.e. the evolution of informal hierarchy.

4.1 Contribution

We demonstrate in this chapter that the organisational benefit of hierarchy can drive the evolution of leader and follower behaviours and ultimately, the transition from small egalitarian to large hierarchical groups. We show that informal hierarchy can evolve *de novo* in the presence of low initial inequality and increasing returns to scale, which are two reasonable assumptions for small-scale societies as observed before the Neolithic transition. To the best of our knowledge, it is the first formal demonstration that voluntary theories of hierarchy can explain the emergence of large-scale informal hierarchy, defined by individuals' behaviour rather than by established political institutions.

4.2 Publications

The majority of the work in this chapter has been published as:

- Cedric Perret, Simon T.Powers and Emma Hart, *Emergence of hierarchy from the evolution of individual influence in an agent-based model*, Proceedings of Artificial Life Conference 2017, MIT Press, 2017

In addition, a portion of the work presented in this chapter has been submitted as:

- Cedric Perret, Emma Hart and Simon T.Powers, *From disorganised equality to efficient hierarchy: How does group size drive the evolution of hierarchy in human societies*, Proceedings of Royal Society B: Biological sciences. Submitted in 2020.

4.3 Introduction

From companies to political parties, organisations tend to follow an “iron law of oligarchy”, in which larger and more productive groups switch to hierarchy where a few individuals possess most of the political power, resources and influence (Michels, 1911). Despite this transition being well known, it is still hard to explain why human groups follow this general trend. As seen in Chapter 2, the absence of coercive means and the long period of egalitarianism (Boehm, 2001) preceding the transition to hierarchy suggests that this transition was voluntary. Functional theories propose that hierarchy provided an important benefit to the group, thus explaining its emergence. Previous work have shown the evolution of leaders as monitors (Hooper et al., 2010) or contributors (Gavrilets and Fortunato, 2014) but there is limited work exploring the role of leader as an organiser. Yet, this role of organiser is particularly interesting because it also gives gives a mean for leaders to bias collective decisions and monopolise resources.

We have shown in Chapter 3 that leaders facilitate group organisation by reducing the time a group spend to reach a consensus. But showing this benefit is not enough to explain the emergence of hierarchy because leaders often enjoy a preferential access to resources (Flannery and Marcus, 2012; Hayden, 2001) and mating partners (Zeitzen, 2008; Summers, 2005). Functional explanations for the emergence of hierarchy suggest that the group benefit brought by hierarchy would be enough to overcome individual selection driving everyone to become a leader rather than a follower (Spisak et al., 2015; Powers and Lehmann, 2014). Yet, there is a conflict between individual and group interests, which makes this condition not trivial (Frank, 1998). A key element to solve this puzzle is the scalar stress, which describes the fact that the cost of organisation scales up with group size (Johnson, 1982). The increase in group size kicked off by agriculture and sustained by subsequent technological innovations, could have amplified the organisational benefit of hierarchy. This relation between size and social organisation appears in the strong correlation between group size and the socio-cultural complexity of societies, e.g. the number of political units, (Johnson, 1982; Carneiro, 1967), number of organisational traits (Carneiro, 1967) or probability of group fission (Alberti, 2014). On one side of the range, small whale hunters have one single coach to coordinate group hunting (Friesen, 1999). On the other extreme, complex states or companies have dozens of politicians and managers who are fully dedicated to the task of organising.

Recent work has shown that scalar stress can drive the evolution of institutional hierarchy, i.e. with an appointed leader, because of a feedback loop between the formation of hierarchy which increases production and subsequently group size, and group size which increases the need for hierarchy (Powers and Lehmann, 2014). Yet, the lack of a mechanistic model describing the effect of hierarchy on group decision-making has limited further investigation of scalar stress and its role in the evolution of hierarchy.

In particular, human groups also exhibit informal hierarchy where leaders and followers are defined by their intrinsic characteristics, either physical e.g. height (Berggren et al., 2010), or psychological e.g. talkativeness, charisma (Judge et al., 2002). Unlike the institutional hierarchy assumed in previous work (Powers and Lehmann, 2014), informal hierarchy does not require political institutions and thus is a strong candidate to explain the first emergence of hierarchy. On the other side, informal hierarchy poses an important challenge as it lacks of a dedicated institution which can enforce hierarchy, and in particular counteract the pressure pushing everyone to become a leader.

This unexplored gap comes from the fact that models of group decision-making and models of evolution require a compatible description of hierarchy. In the Chapter 3, we have described leader and followers by their influence and we have shown how a skewed distribution of influence can lead to a faster consensus. We now incorporate this previous model into an evolutionary model simulating the evolution of influence. The population is structured in patches and within a patch, individuals organise together to produce a collective good. The time to reach consensus determines the cost of organisation, and the influence of an individual on the final decision determines that individual's share of the collective good. The group size varies as a function of the resources of the group and groups compete indirectly by differential migration. Using this model, we aim to answer the following question

Research question. *Can the organisational advantage of a skewed distribution of influence drive the evolution of individuals toward leader and followers behaviours even if it creates inequality?*

4.4 Model definition

4.4.1 Model outline and life cycle

As a reminder, individuals were previously defined by their opinion x and their influence α. The trait α carried by individuals is now an evolving trait. The influence of an individual can now take any value between $[0, 1]$ rather than the value of one of the two profiles defined in Chapter 3. We make the choice of a continuous trait so we do not constraint the possible distribution of influence evolving. Although a division into two profiles, leader and follower, is commonly seen in real world, it has to emerge in this model. The values of the trait α are initially sampled from the uniform distribution between $[0, 1]$. The trait α is transmitted vertically from parent to offspring, e.g. by social learning, as is common in hunter-gatherer groups (Hewlett et al., 2011) and modern societies (Cavalli-Sforza et al., 1982). The trait α mutates following a mutation rate of μ. As α is assumed to be at least partly cultural, we assume a mutation rate higher than for a classical genetic trait. When a mutation occurs, a random value is sampled from a truncated Gaussian distribution centred on the current value of the trait, with variance σ_{m}. The opinion x describes a generic opinion of an individual on how to realise a collective task e.g. next raid target, plan of an irrigation system or value of a law. The values of opinion x are sampled from the uniform distribution between $[0,1]$ at each generation. That is because we assume that the tasks tackled by the groups are different at each generation, and so opinions are not heritable. We describe social organisation as a distribution of influence and use opinion formation to link this distribution back to the cost of organisation as in Chapter 3. Egalitarian to highly hierarchical groups are represented by an equal to strongly skewed distribution of influence α. We study the evolution of α using a classic island model with a population of individuals that is subdivided into a finite number of patches, N_{p} (Wright, 1931). The life cycle consists of discrete and non-overlapping generations, where in each generation the following occur: 1. collective decision-making about how to perform a task; 2. performance of the collective task; 3. distribution of resources obtained from the task; 4. reproduction; 5. migration. The first three steps determinate the success of an individual, which we denote by its fitness w. In short, the fitness of an individual depends on its share of the additional resources produced by the collective task, discounted by the cost of organisation. The cost of organisation and the share of individuals result from the collective decision-making 4.3 and 4.5.

4.4.2 Reproduction

The fitness of an individual is translated into a number of offspring, which is drawn from a Poisson distribution centered on the fitness w. After reproduction, offspring individuals migrate with a probability equal to a fixed migration rate m. Migrating individuals enter a patch chosen at random from the population (excluding their natal patch). More formally, the fitness w of individual i on patch j at time t is described by the following equation:

$$w_{ij}(t) = \frac{r_{\mathrm{a}}}{1+\frac{N_j(t)}{K}} + r_{\mathrm{b}ij}(t). \tag{4.1}$$

where $N_j(t)$ is the total number of individual on patch j. The fitness of an individual is the sum of (i) an intrinsic growth rate r_{a} limited by the carrying capacity K, and (ii) an additional growth rate resulting from the extra resources produced by the collective task, $r_{\mathrm{b}ij}(t)$. The additional growth rate $r_{\mathrm{b}ij}(t)$ is not limited by the carrying capacity, but the competition between individuals is taken into account during the distribution of collective resources. It is calculated as follows:

$$r_{\mathrm{b}ij}(t) = \beta_{\mathrm{r}}(1-e^{-\gamma_{\mathrm{r}}(B_j(t)p_{ij}(t))}). \tag{4.2}$$

The term $r_{\mathrm{b}ij}(t)$ is calculated from a logistic function described by γ_{r} and β_{r}, respectively the steepness and the maximum of the increase in growth rate induced by the additional resources. The additional resources are given by the total amount of benefit, $B_j(t)$, multiplied by the share the individual receives, $p_{ij}(t)$. The increase of the growth rate follows a logistic relation because of the inevitable presence of other limiting factors.

4.4.3 Collective decision-making and collective task

To produce the additional resources $B_j(t)$, individuals first undergo a collective decision-making process on their patch, as defined in the Chapter 3. As a reminder, the collective decision-making is simulated by an opinion formation model, which describes a sequence of discussions between individuals until consensus is reached. After consensus is reached, all individuals on a patch take part in the collective task which produces an amount of extra resource $B_j(t)$:

$$B_j(t) = B_j(t-1)S + \frac{\beta_\mathrm{b}}{1 + e^{-\gamma_\mathrm{b}(N_j(t) - b_\mathrm{mid})}} - C_\mathrm{o} * . \tag{4.3}$$

The benefit is calculated from a sigmoid function described by β_b, b_mid and γ_b, respectively the maximum, the group size at the sigmoid's midpoint, and the steepness of the increase in the benefit induced by additional participants. We make the assumption of increasing returns to scale in which additional participants increase the benefit superlinearly (Pindyck and Rubinfeld, 2001). But as is standard in microeconomic theory, we also make the conservative assumption that the benefit of the collective task eventually has diminishing marginal returns which overcomes the increasing returns to scale because of other limiting factors (Pindyck and Rubinfeld, 2001). To capture the transmissibility of resources (Mattison et al., 2016), we assume that a surplus S of the benefit is passed to the next generation. The extra resources are discounted by the cost of organisation C_o

$$C_\mathrm{oj}(t) = t_j^* C_t \tag{4.4}$$

The cost of organisation comes from the time dedicated to organisation t^* instead of carrying out the actual task, i.e. it is an opportunity cost. This cost is modulated by a parameter C_t, which describes the time constraints on group decision-making. The parameter C_t depends on the pressure of time on the task, for instance, the speed of depletion of resources or the need to build defences before an enemy arrives. To avoid studying the effect of social strategy in the collective task, which has already been extensively studied in the evolution of cooperation literature (West et al., 2007), we consider that all the individuals on a patch are willing to participate in the collective task once a decision is reached. The collective task simulates the numerous cooperative tasks realised during the lifetime of an individual. It can encompass many actions such as warfare battle or construction of an irrigation system.

4.4.4 Distribution of common resources

The resources obtained from the collective task are distributed among all individuals on the patch. We want to test if hierarchy can emerge even if leaders receive a higher share of the collective resources, which selects against individuals becoming followers. However, leaders are not clearly designated in informal hierarchy. We assume that in the absence of coercive means, individuals can only increase their share by biasing the collective decisions towards their own interests and thus, the share of an individual $p_{ij}(t)$ is a function of its realised influence α_r such that:

$$p_{ij}(t) = \frac{1 + d\alpha_{r(ij)}(t)}{\sum_{i=1}^{N_j}(1 + d\alpha_{r(ij)}(t))}. \tag{4.5}$$

The asymmetry of the distribution of the resources is modulated by a parameter d, which represents the level of ecological inequality. For $d = 0$, a patch is totally egalitarian and the influence of an individual does not affect the share of that individual. Such a scenario is close to the society of pre-Neolithic hunter-gatherers (Boehm, 2001). It is assumed for simplicity that d is the same for all patches, and is determined for example by the state of technology, such as food storage and military technologies. Nevertheless, different patches can have more or less despotic distributions of resources due to different distributions of α_r values. The realised influence of an individual $\alpha_{r(ij)}$ is calculated from the difference between an individual's initial opinion and the final decision and measures how much the final decision is close to the individual's interest:

$$\alpha_{r(ij)} = 1 - |x_{ij}(t = 0) - x_j^*| \tag{4.6}$$

4.5 Results

We use this model to answer the following question:

Research question. *Can the organisational advantage of a skewed distribution of influence drive the evolution of individuals toward leader and followers behaviours even if it creates inequality?*

The model defines a stochastic process for the evolving trait, and for the reproduction and decision-making processes. Because of the nonlinearities of the model, which result from the interactions of all of the variables, we analyse it using replicated numerical simulations.

We define hierarchy as a positively skewed distribution of influence α, which describes a minority of individual with high influence α and a majority of individuals with low influence α. We use skewness rather than fitting and estimating the parameters of a particular distribution e.g. bimodal distribution, for two reasons. First, skewness is more general in the sense that it does not make assumption on the distribution observed. Second, skewness is easier to calculate because it does not need to measure how much the distribution fits the data and to estimate the parameters of a distribution. The skewness is measured by the Pearson's moment coefficient of skewness $\mu_{3\alpha}(t)$:

$$\mu_{3\alpha}(t) = E[(\frac{\alpha(t) - \bar{\alpha}(t)}{\sigma_\alpha(t)})^3] \tag{4.7}$$

with $\bar{\alpha}(t)$ the mean of α at time t and σ_α(t) the standard deviation of α at time t. We focus on the effect of the following parameters: (i) the level of ecological inequality d because it is the main limit to informal hierarchy and (ii) and the number of listeners n_l, which affects the intensity of scalar stress (as seen in Chapter 3). We also explore the effect of (i) the time constraints on group decision-making C_t because it affects the benefit provided by hierarchy, (ii) the migration rate m, which affects the population structure and (iii) the absence of transmission of resources from one generation to another ($S = 0$). The default values for the parameters studied, unless otherwise specified, are for the level of inequality $d = 1$, the number of listeners $n_\mathrm{l} = 30$, the time constraints on group decision-making $C_\mathrm{t} = 2$, the migration rate $m = 0.05$ and the fraction of resources transmit to next generation $S = 0.9$. The results presented are the average across patches when the result is a function of generations. and the average across patches, generations and simulations when the result is a function of a parameter. The error-bars represent the standard error from the mean across replicates. The default parameter values used in the simulations, unless otherwise specified, are for the number of patches $N_\mathrm{p} = 50$, the initial number of individuals on each patch $N_j(0) = 50$, the carrying capacity $K = 50$, the intrinsic growth rate $r_\mathrm{a} = 2$, the increase of benefit as a function of size (maximum, steepness, mid-point) $\beta_\mathrm{b} = 10000$, $\gamma_\mathrm{b} = 0.005$, $b_\mathrm{mid} = 500$. These values are chosen in order to allow the transition between tribe size (50 to 100 individuals) to small chiefdom size (500 individuals) (Earle, 1987). The default values for the increase in growth rate due to additional resources (maximum and steepness) are $\beta_\mathrm{r} = 3$, $\gamma_\mathrm{r} = 0.025$. They are chosen so that additional resources lead to a clearly increased fitness. The remaining default parameters are for the consensus threshold $x_\theta = 0.05$, the mutation rate $\mu_\mathrm{m} = 0.01$, the mutation strength $\sigma_\mathrm{m} = 0.01$.

Figure 4.1 presents the evolution of the distribution of influence and group size as a function of generations for a single run. The results show that despite the wide range of possible distribution of influence, the population evolves towards hierarchy, i.e. a minority of leaders with high influence and a majority of followers with low influence. In the meantime, the population grows to a large group size. Within a patch, informal hierarchy also evolves but the proportion of leaders and followers vary. The result is stable across replicates and in the long term as shown by Figure 4.2.A . At the start of the simulation, groups have a skewness close to 0 and a small group size because the values of influence are randomly initiated. Figure 4.2.A demonstrates that skewness increases with time and remains at a positive value along generations. The positive

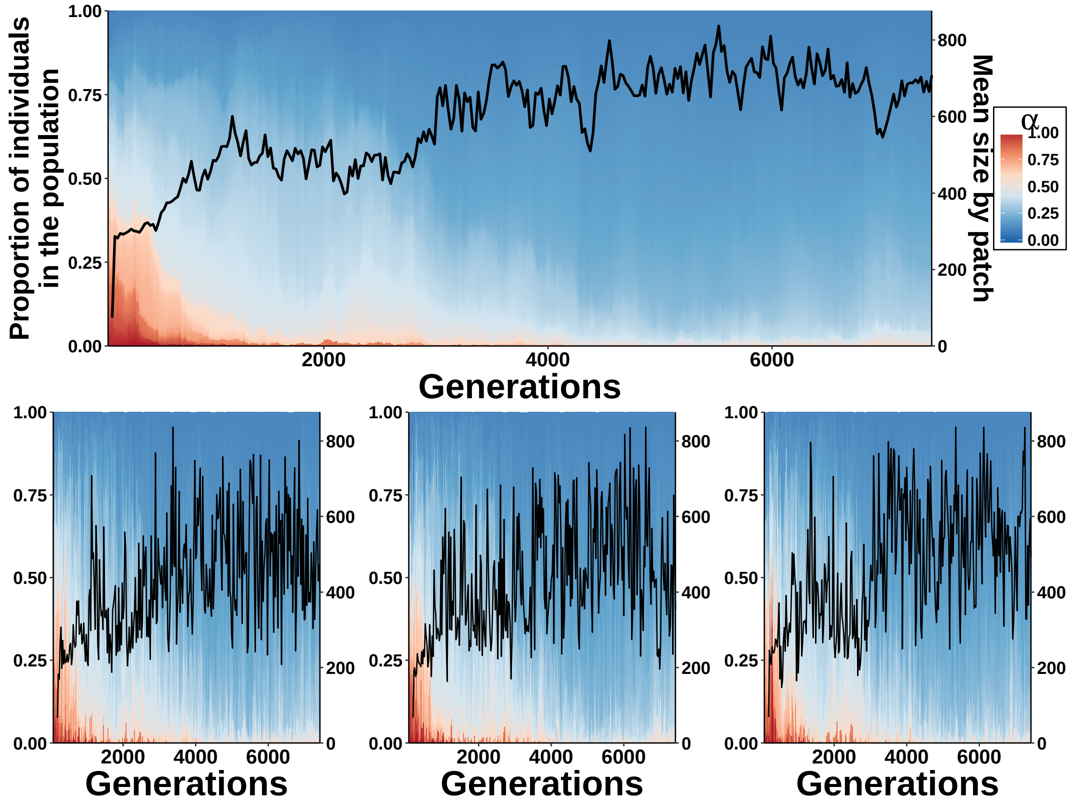

Figure 4.1: Evolution of the distribution of influence α, and evolution of group size as a function of generations for the whole population (top) and three different patches (bottom). The plot represents results for a single run.

skewness reflects a majority of individuals with low influence - followers - and a minority of individuals with high influence - leaders. This result is also present in absence of intergenerational transmission of resources ($S = 0$) as seen in Figure 4.3. Overall, this result shows that hierarchy can emerge from the evolution of individual behaviour and thus, informal hierarchy provides a clear evolutionary advantage.

The benefit of an efficient hierarchical organisation appears in Figure 4.2.C . It shows that over generations, the consensus time and the total amount of resources both increase. This is because group size increases and leads to more resources being produced due to increasing returns to scale. It also results in a greater difficulty to organise. However, it can be observed in Figure 4.2.C that the increase in consensus time stabilises before the end of the increase in extra resources. This is because individuals have adopted an informal hierarchy and can maintain a low cost of organisation as the group size and the production of resources continue to increase. The benefit of hierarchy depends of the time constraints C_t which translates the consensus time into an opportunity cost of organisation. Figure 4.4 shows that the level of hierarchy is proportional to the time constraints. For a low level of time constraints, the benefit of hierarchy has a negligible effect on organisation and group production and thus, hierarchy does not evolve. For tasks with strong time constraints, e.g. warfare, the benefit of hierarchy is amplified and a strong hierarchy, i.e. high skewness of the distribution of influence, evolves.

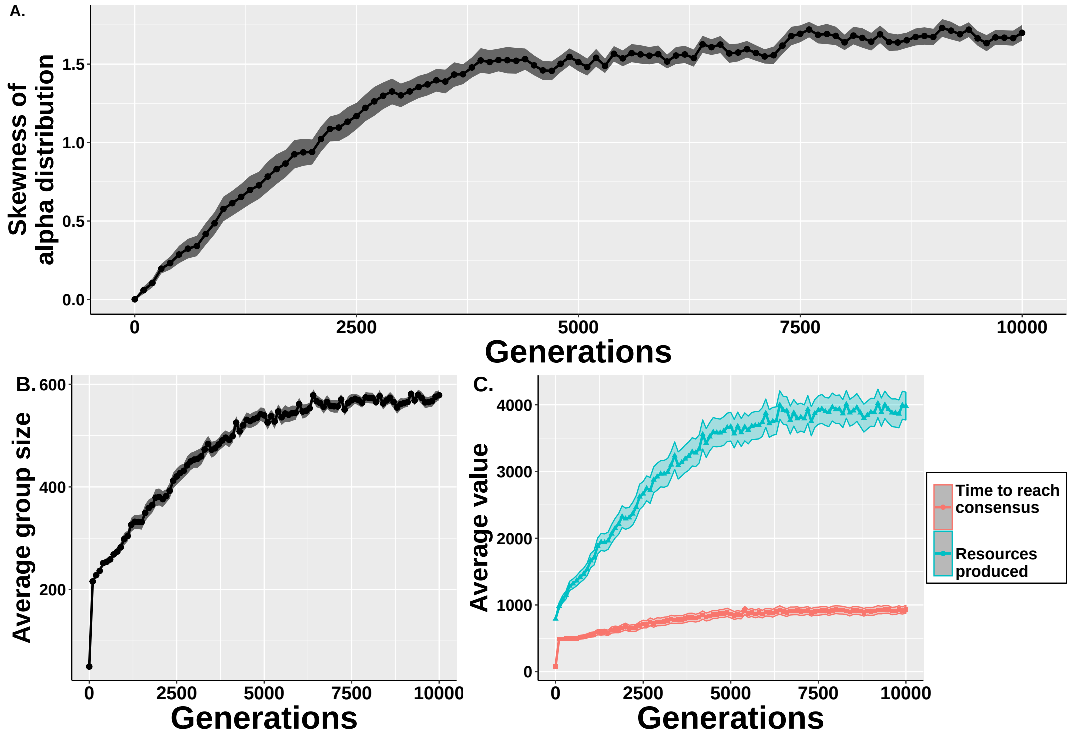

Figure 4.2: Evolution of (A) the average skewness of distribution of influence α, (B) average group size, (C) average time to reach consensus (red) and average amount of resources produced (blue) as a function of generations. Informal hierarchy is represented by a positive skewness. The values presented are the average across patches, 5000 generations and 32 replicates. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions.

Hierarchy evolves because it reduces the cost of organisation and thus provides the creation of surplus in group production. These surplus resources are distributed among the individuals and increase the number of offspring individuals produce. It results in hierarchical groups being larger and exporting a larger number of migrants than groups without hierarchy. Most of these migrants are followers because most of the population within a hierarchy are followers. Ultimately, it spreads hierarchical organisation to other groups and at the level of population, it creates a stable distribution of individuals with low and high influence.

Importantly, this process occurs even when the emergence of hierarchy creates inequality. Inequality limits the development of hierarchy because it increases the number of offspring leaders produce and potentially drives all individuals within a group to develop high influence. This is because leaders will more often bring the group decision close to their preferences and thus receive a higher share of the resources produced. This effect can be seen in Figure 4.5.A, which shows that a higher level of inequality reduces the skewness of the distribution of influence. This effect is limited by the competition between leaders. In the presence of multiple leaders, a leader can get a lower share of the resource than followers if the group becomes convinced by another leader during the decision-making process. In this case, the“losing” leaders are further

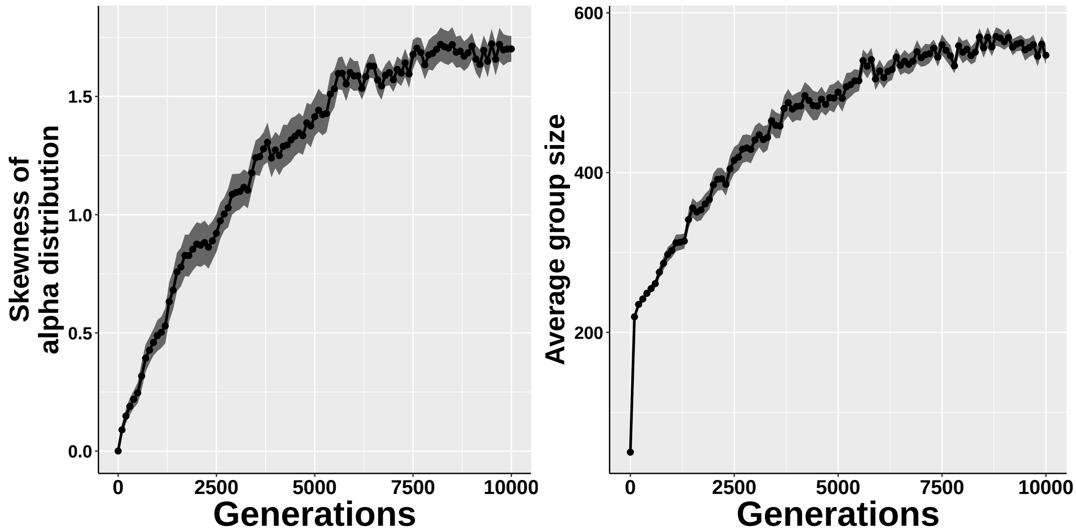

Figure 4.3: Evolution of the average skewness of distribution of influence α and the average group size as a function of generations in the absence of intergenerational transmission of resources ($S = 0$). Reducing the transmission of resources also decreases the total amount of resources available. To distinguish the effect of the transmission of resources from a decrease of resources produced, we maintain the amount of resources produced to be the same value than simulations with $S = 0.9$, by multiplying the total amount of resources produced $B_j(t)$ by 1.9. The values presented are the average across patches, 5000 generations and 32 replicates. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions.

from the final decision because they are harder to convince. However, the fact that hierarchy does not evolve for high levels of inequality shows that this competition is not always enough to stop the increase in number of leaders and the collapse of hierarchy. The second reason explaining the evolution of hierarchy despite inequality is that even if leaders receive more resources, followers still get a higher amount of resources and offspring than they would in a group without hierarchy. Large groups produce more resources due to increasing returns to scale, e.g. division of labour and specialisation.

We have seen previously that hierarchy reduces the time to reach consensus but it also provides a second main advantage to group organisation: it reduces scalar stress. To test the importance of this factor in the evolution of hierarchy, we look at the skewness of the distribution of influence for different values of number of listeners, N_l. Figure 4.5.B shows that high scalar stress, i.e. low number of listeners N_l, leads to the evolution of a more skewed distribution of influence. On the other hand, a low scalar stress, i.e. here represented by a high number of listeners N_l, leads to the disappearance of hierarchy. This result shows that the benefit of reducing scalar stress is a crucial factor in the evolution of hierarchy. This is because scalar stress creates a positive feedback loop by which hierarchy increases its own benefit. On the one hand, an efficient hierarchical organisation allows a group to produce a larger amount of resources and hence to reach a larger size. On the other hand, hierarchy provides a stronger advantage as group size increases because the cost of organisation increases less in hierarchical groups than in

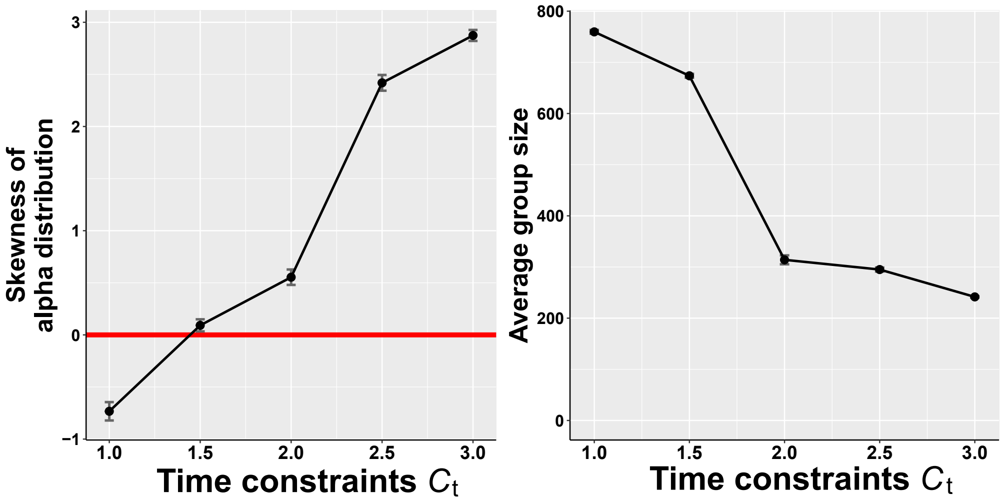

Figure 4.4: Average skewness of the distribution of influence α and average group size as a function of the time constraints on group organisation C_t. The values presented are the average across patches, 5000 generations and 32 replicates. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions.

acephalous groups. There is a feedback loop between hierarchy leading to larger group size, and larger group size increasing the benefit of hierarchy. Eventually, this feedback loop comes to an end due to diminishing marginal returns i.e. other limiting factors than group size. Yet, this feedback loop amplifies the benefit that hierarchy provides to the group members and favours its evolution.

To summarise, social organisation is the equilibrium between two opposing forces, competition within groups where inequality pushes individuals to evolve high influence, and competition between individuals of different groups where efficient group organisation pushes most individuals to evolve low influence. To give more insight into the selection forces in play, we use the kin selection framework and describe the benefit that the trait provides to the individual carrying the trait (direct benefit) and the benefit that the trait provides to related individuals (indirect benefit) (Frank, 1998). Hierarchy provides one direct and one significant indirect benefit to followers compared to individuals in acephalous groups. First, hierarchy provides a direct benefit to followers because it increases the amount of surplus resources produced and thus, it increases the fitness of followers. Second, hierarchy provides an indirect benefit to followers because it increases the group size and hence the amount of resources produced in the following generation. This, in turn, increases the fitness of followers' offspring [1]. The contribution of each benefit is hard to distinguish but their role can be examined by investigating the effect of high migration rate, which suppresses population structure and hence any indirect benefit to offspring on the same patch. Figure 4.6 shows that, considering moderate time constraints, a high migration rate leads to the disappearance of hierarchy

[1] Note that hierarchy also provides an indirect benefit to followers at the same generation because it increases the amount of resources received by related individuals. However, this benefit is negligible in large groups (Frank, 1998).

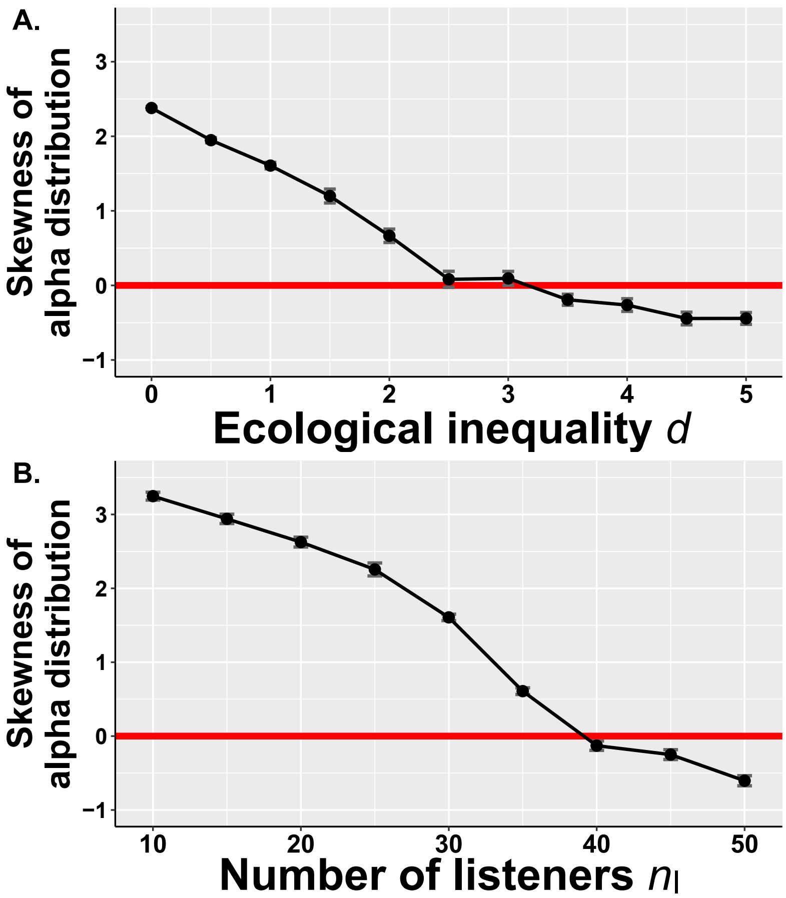

Figure 4.5: Average skewness of the distribution of influence α as a function of the level of ecological inequality d and the number of listeners n_l. The values presented are the average across patches, 5000 generations and 32 replicates. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions.

at equilibrium. This highlights the importance of the indirect benefit to offspring that remain on the patch in sustaining hierarchy. On the other hand, Figure 4.7 shows that hierarchy evolves for any migration rate if the the time constraints are high. In this case, the direct benefit is high enough to overcome the cost of economic inequality. In conclusion, hierarchy can evolve when time constraints are high through the immediate direct benefit of producing extra resources, but the indirect benefit resulting from the feedback loop between hierarchy, group size and scalar stress allows hierarchy to evolve over a much wider range of conditions.

4.6 Discussion

The origin of leadership in human societies is still hard to comprehend. In particular, leaders tend to exploit followers, which should theoretically limit the evolution of followers. Group size and the resultant scalar stress have been proposed as a crucial factor to explain the emergence of hierarchy from previously egalitarian groups (Johnson, 1982; Powers and Lehmann, 2014). Yet, the investigation of this hypothesis in models

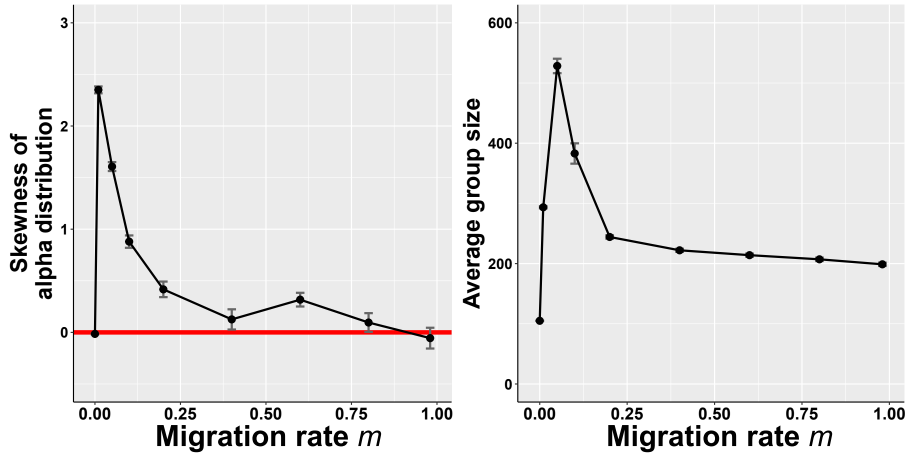

Figure 4.6: Average value of Pearson's moment coefficient of skewness of the distribution of influence α and average group size across 5000 generations and across 32 replicates as a function of migration rate m.The time constraints on group organisation is moderate $C_t = 2$. The parameter ranges from $m = 0$ i.e. each group is independent to $m = 1 - \frac{1}{N_p}$ i.e. a well-mixed population. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions. The error bars represent the standard error from the mean between replicates.

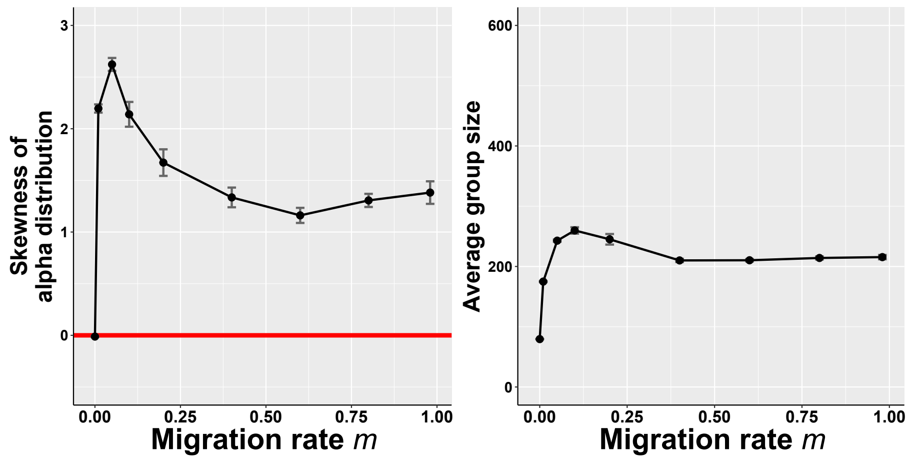

Figure 4.7: Average value of Pearson's moment coefficient of skewness of the distribution of influence α and average group size across 5000 generations and across 32 replicates as a function of migration rate m. The time constraints on group organisation is high $C_t = 3$. The parameter ranges from $m = 0$ i.e. each group is independent to $m = 1 - \frac{1}{N_p}$ i.e. well-mixed population. The simulations are run for 10000 generations and the first 5000 generations are ignored to limit the effects of initial conditions. The error bars represent the standard error from the mean between replicates.

of evolutionary dynamics has been limited so far. To fill this gap, we have described group social organisation by the distribution of an individual trait, the influence. We have integrated a mechanistic model of social dynamics within an evolutionary model to test if influential leader and influenceable follower behaviours can emerge by evolutionary processes at the individual level. Our results demonstrate that this benefit provides enough selective pressure to lead to the emergence of informal hierarchy from bottom-up evolution of individual behaviours, even if this hierarchy results in inequality.

The model developed by Powers and Lehmann (2014)] shows that leadership as an institution can evolve if hierarchy leads to an increase in group size (Powers and Lehmann, 2014). Our model has independently confirmed that this prediction holds even when leadership emerges bottom-up from the evolution of traits affecting individual influence. To understand whether leadership could have emerged first from bottom-up individual behaviour and then later become institutionalised, or whether the opposite is true, is still an important question to fully understand the evolution of leadership. This model shows that the former is a plausible scenario and suggests further investigation of the interactions between bottom-up and top-down creation of leadership roles in societies. More broadly, our model is in line with theoretical works that propose a voluntary emergence of hierarchy and joins previous works that focused on a particular task, e.g. building irrigation systems (Wittfogel, 1957) or maintaining cooperation by policing (Hooper et al., 2015).

Our findings predict that the level of hierarchy, i.e. skewness of the distribution of influence, should increase with group size and with the cost of organisation of the tasks tackled by the group. A previous review of ethnographic data presents evidence that political complexity, i.e. the number of political units, (Johnson, 1982; Carneiro, 1967), number of organisational traits (Carneiro, 1967) or probability of group fission (Alberti, 2014). For example, the Inuit population on coastal North Alaska is composed of large groups relying on bowhead whale hunting, a complex coordination task. These populations are thus under high scalar stress and exhibit a strong hierarchy with leaders who own the hunting equipment and decide the distribution of resources. In comparison, smaller groups of Inuits living on the Mackenzie Delta rely on personal hunting and have a less hierarchical organisation (Friesen, 1999). Other than scalar stress, our findings predict that low initial inequality and increasing returns to scale are necessary. Much anthropological evidence shows that inequality was strongly limited in pre-hierarchical societies because of anti-authoritarian mechanisms, e.g gossip, ostracisation; and the absence of coercive institutions, e.g. dedicated armies and tax collection (Boehm, 2001). Increasing returns to scale is commonly observed in human collective actions and results from synergistic interactions between individuals such as division of labour and specialisation (Powers and Lehmann, 2017). Archaeological evidence suggests that agriculture could have provided Neolithic society with such scalable means of production (Bocquet-Appel, 2011).

Put in perspective, the results of the model show that informal hierarchy evolves when the cost of organisation is high enough. Unfortunately, measures of cost of organisation are limited, in particular in past societies. Yet, a collective task can carry high cost of organisation because it involves a very large number of coordination problems, e.g. distribution of the roles, technical details, time management, etc.. In addition, the difficulty to organise these tasks is amplified by the number of people involved, which unlike the model presented can go up to hundred thousands, e.g. kingdoms, or millions, e.g. European Union. Importantly, not only collective tasks incur a cost of organisation. For instance, institutional rules are designed by collective decision-making, and require to be often updated because their efficiency depend of many dynamic variables, e.g. social, environmental or historical factors (Ostrom, 1990). The development of a large number of institutional rules at the Neolithic transition could also have increased the need for efficient organisation (Powers et al., 2016) Nevertheless, the generality of a scenario where organisation drives the evolution of hierarchy needs to be better estimated with further work exploring the relation between individual behaviours, group size and cost of organisation either in laboratory experiments or in real-world human groups.

As discussed in Chapter 3, the opinion formation model is a simplification of collective decision-making and is missing some crucial parts of group organisation, e.g. individual knowledge, network structure. However, it is based on simple and supported assumptions and already captures the benefit of hierarchy in group organisation. It is a first step to move from a benefit of hierarchy that is simply assumed in a model to a more mechanistic explanation. In addition, this model provides a link between the well developed fields of evolutionary dynamics and social dynamics, which we believe could provide important insights on the evolution of social organisation in human societies. Further work can develop the opinion formation model and investigate the effects of additional factors on the evolution of informal hierarchy.

We have considered here a model of multi-level selection by propagation where the competition between groups is captured by the difference in number of migrants, and hierarchy is spread by demic diffusion. This assumption is supported by evidence showing that agriculture would have spread by demic diffusion rather than by cultural transmission between groups (Pinhasi et al., 2005). Another possibility to model the evolution of structured populations is to model groups as the reproductive entities (sometimes called models of multi-level selection 2 Okasha 2008), by considering that groups can undergo fission or fusion, e.g. by conquest. This formalisation has the benefit of capturing intergroup conflict, here ignored. However, ignoring intergroup conflict is conservative because conflicts between groups would only increase the competition between individuals of different groups and thus lead to the same qualitative result. In addition, the model presented here still gives insights on the role of intergroup conflict. It is likely that warfare would favour hierarchy because it is a task with high time constraints and it results in larger group size, which are both factors that we have shown to correlate with hierarchy. In a similar way, we do not consider that groups can disappear and get reformed by migration from the first group, i.e. propagule model. Although propagule models apply well to organisms such as bacteria, it make the assumption that humans groups can often collapse. However, our choice is conservative because a propagule model would also increase the selection pressure at the group level and thus would favour the evolution of hierarchy. Finally, we considered that group size and productivity can differ among patches (as observed in real-world). This assumption is important because it reduces the competition among related individuals and allows the indirect benefit of the trait to influence selection (which otherwise is cancelled out by the competition among related individuals Taylor 1992).

Our model, combined with previous research (Powers and Lehmann, 2014), shows that a functional hypothesis is a plausible scenario to explain the transition to hierarchy. Expanding human groups switch to hierarchy in an informal or institutional way (Powers and Lehmann, 2014) to limit the costs of large-scale organisation. However, if both forms of hierarchy provide a benefit to group organisation, institutional hierarchy requires costly political institutions. Thus, why does institutional hierarchy is so prevalent despite its additional costs? We investigate this question in the next chapter.

Fifth Chapter

The evolution of institutionalised hierarchy

Human social hierarchy has the unique characteristic of existing in two forms. Firstly, as an informal hierarchy where leaders and followers are implicitly defined by their personal characteristics, and secondly, as an institutional hierarchy where leaders and followers are explicitly appointed by group decision. Although both forms can reduce the time spent in organising collective tasks (as shown in Chapter 4 and Powers and Lehmann 2014), institutional hierarchy imposes additional costs. It is therefore natural to question why it emerges at all. We propose that the key difference lies in the fact that institutions can create hierarchy with only a single leader, which is unlikely to occur in unregulated informal hierarchy. In this chapter, we investigate if this difference can explain the evolution of cultural preferences toward institutional hierarchy, despite its additional costs.

5.1 Contribution

In this Chapter 5, we demonstrate that individuals evolve cultural preferences towards institutional hierarchy because (i) it provides a greater organisational advantage than informal hierarchy, (ii) reduces the detrimental effect of group size and (iii) is more resilient in the face of inequality on the time spent to organise collective actions.

5.2 Publication

The majority of the work in this chapter has been published as:

- Cedric Perret, Emma Hart and Simon T.Powers *Being a leader or being the leader: The evolution of institutionalised hierarchy*, Proceedings of Artificial Life Conference 2019, MIT Press, 2019

5.3 Introduction

Why do humans choose their leaders? A meta-analysis of sixty independent studies shows that leadership effectiveness is not always correlated with leadership emergence (Judge et al., 2002). In other words, groups sometimes choose incompetent individuals as leaders. For instance, experiments on leader choice showed that *"evaluations of beauty explain success in real elections better than evaluations of competence, intelligence, likability, or trustworthiness"* (Berggren et al., 2010). Yet, despite these risks, most modern human hierarchies spend time and resources to explicitly choose leaders, even if efficient leaders are already designated by their characteristics and skills.

Human social hierarchy has the unique characteristic of existing in two forms (Pielstick, 2000). Firstly, as an *informal* hierarchy where leaders and followers are implicitly defined by their personal characteristics, and secondly, as a *formal* hierarchy where leaders and followers are explicitly appointed by decision. We call the formal hierarchy here *institutional* hierarchy to stress that it is supported by institutional rules, which are created by group decision and actively enforced by monitoring and punishment (Ostrom, 1990; Hurwicz, 1996). The emergence of informal (as seen in Chapter 4 or institutional hierarchy (Powers and Lehmann, 2014) can both be explained by the fact that they reduce costs of organisation. However, institutional hierarchies are surprisingly pervasive in modern societies, given that they carry additional costs in comparison to informal ones. First, institutions need to be created (and updated) and thus institutional rules need to be agree upon. As we have seen in Chapter 3, collective decision-making can be a long process and is likely to be even longer for a sensitive topic such as the distribution of power. Second, institutions need to be enforced. For example, individuals trying to usurp the power need to be punished.

We propose that a key to this puzzle lies in the particularity of institutions which allow humans to hand-tune their behaviours, e.g. by designating a single leader, in comparison to informal hierarchies in which leaders emerge through evolutionary processes. In informal hierarchies, the mutations combined to the conflicting selection forces create variations in individual traits and the number of leaders. As shown in chapter 3, hierarchy with a single and strongly influential leader in comparison to multiple leaders hierarchy leads to bigger reductions in (i) the time to consensus, (ii) the variation in the time to consensus, and (iii) the increase in time to consensus as group size increases. However, it remains unclear whether this difference could drive the appearance of institutional hierarchies when informal hierarchy is in place.

Currently, independent explanations for the evolution of informal (Chapter 4) and institutional hierarchy (Powers and Lehmann, 2014) have been provided, but there is no model that investigates the competition between these two forms of social organisation. To fill this gap, we modify the evolutionary model developed in Chapter 4 such that individuals can choose between informal social organisation where the influence of individuals is defined by individuals' characteristics, or institutional social organisation where the influence of individuals are defined by the institution. Using this model, we aim to answer the following question

Research question. *Can the organisational advantage of single leader hierarchy drive the evolution of preferences toward institutionalised hierarchy despite the additional cost of institutions?*

5.4 Model definition

We extend the evolutionary model presented in chapter 4 to integrate institutional hierarchy. To do so, we define political organisation as the process by which leaders and followers are defined. The political organisation of a group can either be *informal*, i.e. leaders and followers are defined by default by individual characteristics, or *institutional*, i.e. leaders and followers are defined by group decision.

5.4.1 Model outline and life cycle

Individuals are still described by a value of influence α as previously. However, the influence is not anymore an evolving trait but is either defined by an individual social personality s in an informal hierarchy, or by their assigned individual social position in institutional hierarchy. Individuals carry two evolving traits: their social personality s and their preference for political organisation h. The trait s represents the intrinsic personality of an individual in a social interaction (e.g. talkativeness, boldness, charisma). In an informal organisation, it defines an individual's influence α and in this case, is equivalent to the evolving trait described in previous chapter 5. In an institutional organisation, the trait s affects the probability to be chosen as a leader. Unlike previous model, the social personality is a discrete trait and can be either dominant $s = 1$, or compliant $s = 0$. Thus, we define social organisation by the proportion of leaders and followers present in a patch. In a similar way, we consider that only two profiles of influence: leader L, and follower F. Each profile has a fixed value of influence α such that $\alpha_{\mathrm{L}} > \alpha_{\mathrm{F}}$. We do this simplification because the results of chapter 4 shows that even when considering a continuous trait, two profiles (leader and follower) emerge. In addition, it simplifies the model to focus more on the evolution of institutional hierarchy. The trait h represents the preference in terms of political organisation of an individual: 0 represents a preference for informal organisation, and 1 a preference for institutional organisation.

The two traits s, h carried by individuals are transmitted vertically from parent to offspring, e.g. by social learning as is common in hunter-gatherer groups (Hewlett et al., 2011). They mutate following a mutation rate of μ. As these traits are assumed to be at least partly cultural, the mutation rate is higher than for a classical genetic trait. When a mutation occurs, the trait value is flipped.

We consider an island model with a population of individuals that is subdivided into a finite number of patches N_p (Wright, 1931). The life cycle consists of discrete and non-overlapping generations as follows:

1. Individuals decide whether to create an institutional hierarchy and appoint a leader (equation 5.1; or defaults to an informal organisation where leaders and followers roles are defined by individuals' personality s. Individuals creating an institutional hierarchy pay a cost c_h.

2. Individuals play a decision-making game on their patch as defined in Chapter 3. The time taken to reach consensus is translated into an opportunity cost of organisation (equation 5.2).

3. After consensus is reached, all individuals on a patch take part in a collective task which produces an amount of extra resource, discounted by the cost of organisation (equation 5.3).

4. The resource obtained from the collective task is distributed among all individuals on the patch. Leaders get a surplus of resources modulated by a parameter d which modulates the inequality between leaders and followers (equation 5.4)

5. Individuals produce a number of offspring drawn from a Poisson distribution, with the mean determined by the resources received (equation 5.5)

6. All individuals of the previous generation perish.

7. Offspring migrate with a fixed probability m. Migrating individuals enter a patch chosen at random from the population (excluding their natal patch).

5.4.2 Political organisation

Each group within a patch is defined by a political organisation h^*. At the beginning of each generation, individuals decide if they want to design an institutional hierarchy and appoint a leader ($h^* = 1$); this occurs if the majority of individuals in the group have a preference toward institutional hierarchy:

$$
\begin{aligned}
h^* = 0 \quad if \quad \frac{1}{N_j(t)} \sum_{i}^{N_j(t)} h_{ij}(t) < 0.5 \\
h^* = 1 \quad if \quad \frac{1}{N_j(t)} \sum_{i}^{N_j(t)} h_{ij}(t) > 0.5
\end{aligned}
\tag{5.1}
$$

In the absence of institutions ($h^* = 0$), a group is organised by default as an informal hierarchy. In an institutional hierarchy, one single leader is randomly selected from the individuals with dominant personality $s = 1$ and its influence is set to α_l. In absence of individuals with dominant personality, the leader is randomly selected from all individuals within the group. The rest of the individuals within the patch adopt a follower profile and their influences are set to α_f (independently of their social personality). In an informal hierarchy, an individual's influence α is defined by its social personality with α_l for dominant individuals $s = 1$ and α_f for compliant individuals $s = 0$. In order to be sustainable, institutions require resources to monitor individuals and punish transgressors (Ostrom, 1990). Thus, individuals creating an institutional hierarchy pay a cost c_h. It is worth noting that we constrain an institutional group to be a hierarchy, but a group can have an informal political organisation with either an egalitarian or hierarchical social organisation.

5.4.3 Organisation by decision-making

Once individuals have chosen their political organisation, they organise a collective task through group decision-making as described in Chapter 3. The consensus time is translated into a cost of organisation:

$$C_{\mathrm{oj}}(t) = t_j^* C_t \tag{5.2}$$

The cost of organisation comes from the time dedicated to organisation instead of carrying out the actual task – groups that take too long to reach a decision may lose resources or pay other opportunity costs. This cost is modulated by C_t, which is a parameter representing the time constraint on decision-making and depends of the limitation of time on the task, for instance, the speed of depletion of resources or the need to build defences before an enemy arrives. We consider here that the final decision reached has no effect on the benefit produced by the collective task – the benefit is only affected by the time taken to reach consensus.

5.4.4 Collective task

At each generation, individuals take part in a collective task and produce additional resources $B_j(t)$:

$$B_j(t) = \frac{\beta_\mathrm{b}}{1 + e^{-\gamma_\mathrm{b}(N_j(t) - b_\mathrm{mid})}} - C_{\mathrm{oj}}(t). \tag{5.3}$$

The collective task simulates the numerous cooperative tasks realised during the lifetime of an individual. It can encompass many actions such as hunting of large game or construction of an irrigation system. The benefit is calculated from a sigmoid function described by β_b, b_{mid} and γ_b, respectively the maximum, the group size at the sigmoid's midpoint, and the steepness of the increase in the benefit induced by additional participants. We assume increasing returns to scale in which additional participants increase the benefit super-linearly (Pindyck and Rubinfeld, 2001). But as is standard in micro-economic theory, we also make the conservative assumption that the benefit of the collective task eventually has diminishing marginal returns which overcomes the increasing returns to scale because of other limiting factors (Foster, 2004).

5.4.5 Distribution of resources

The resources produced by the collective task are distributed between the individuals on a given patch. The share of an individual, $p_{ij}(t)$, is equal to:

$$p_{ij}(t) = \frac{1 + l_i(t)d}{\sum_{i=1}^{N_j}(1 + l_i(t)d)}. \tag{5.4}$$

We simplify the previous model of chapter 4 by considering that leaders ($l = 1$) receive a surplus of resources modulated by the level of ecological inequality d. For $d = 0$, the distribution within a patch is egalitarian and the influence of individuals does not affect the share of each individual. Such a scenario is close to that observed in societies of pre-Neolithic hunter-gatherers. For $d = 1$, leaders receive twice the amount a follower receives. It is assumed for simplicity that d is the same for all patches, and is determined for example by the state of technology, e.g. food storage and military technologies.

5.4.6 Reproduction

After receiving their share of the additional resources, individuals have a number of offspring sampled from a Poisson distribution centred on the individual fitness, w. The fitness of individual i on patch j at time t is described by the following equation, where $N_j(t)$ is the total number of individual on patch j:

$$w_{ij}(t) = \frac{r_a}{1 + \frac{N_j(t)}{K}} + r_{bij}(t) - c_h h_j^* - c_n s_{ij}. \tag{5.5}$$

The fitness of an individual is the sum of an intrinsic growth rate r_a limited by the carrying capacity K, and additional growth rate resulting from the extra resources produced by the collective task, $r_{bij}(t)$. The fitness of individuals with institutional organisation is discounted by a cost of institution c_h, which represents the cost to monitor and enforce the institutional rule. The fitness of dominant individuals is discounted by a cost of negotiation c_n which represents the extra time and resources that an individual with dominant personality allocates to persuade others. The additional growth rate $r_{bij}(t)$ is calculated as follows:

$$r_{bij}(t) = \beta_r(1 - e^{-\gamma_r(B_j(t)p_{ij}(t))}). \tag{5.6}$$

The term $r_{bij}(t)$ is calculated from a logistic function described by γ_r and β_r, respectively the form and the maximum of the increase in growth rate induced by the additional resources. The additional resources are given by the total amount of benefit, $B_j(t)$, multiplied by the share the individual receives, $p_{ij}(t)$. The increase of the growth rate follows a logistic relation because of the inevitable presence of other limiting factors. After reproduction, offspring individuals migrate with a probability equal to a fixed migration rate m. Migrating individuals enter a patch chosen at random from the population (excluding their natal patch).

5.5 Results

We use this model to answer the following question:

Research question. *Can the organisational advantage of single leader hierarchy drive the evolution of preferences toward institutionalised hierarchy despite the additional cost of institutions?*

Because of the non-linearities of the model, which result from the interactions of all of the variables, we analyse it using replicated numerical simulations. The initial values of the social personality of individuals, s are sampled on a discrete uniform distribution on $\{0, 1\}$. The initial values of preference for political organisation h are set to 0 to represent the initial absence of institutions. We focus on the effect of the following parameters: (i) the level of ecological inequality d because inequality limits the evolution of informal hierarchy, (ii) the cost of institution C_h because it is the main limit to the evolution of institutional hierarchy and (iii) the time constraint C_t because it affects the benefit provided by hierarchy. The default parameters are for the consensus threshold $x_\theta = 0.05$, the number of listeners $N_l = 50$, the influence of leaders $\alpha_l = 0.75$ and the influence of followers $\alpha_f = 0.25$. The default parameters used in the simulations, unless otherwise specified, are $N_p = 50$, $N_j(0) = 20$, $K = 20$, $r_a = 2$, $\beta_b = 10000$, $\gamma_b = 0.005$, $b_{mid} = 250$, $\beta_r = 3$, $\gamma_r = 0.05$, $\mu_m = 0.01$ and $m = 0.05$. These parameters are chosen in order to allow the transition between tribe size (50 to 100 individuals) to chiefdom size (500 individuals). Finally, we want to allow for hierarchy even when the political organisation is informal. To do so, we choose a high cost of negotiation C_N which limits the evolution of too many leaders and allows relatively stable informal hierarchy. The results presented are the mean across patches and 32 replicates when the result is as a function of generations; and across patches, 32 replicates and 5000 generations when the results are as a function of a parameter. Where the result is described as a mean, it is the mean value across patches. The error bars represent the standard error from the mean and are not represented when they are too small to be visible (< 5% of the maximum value).

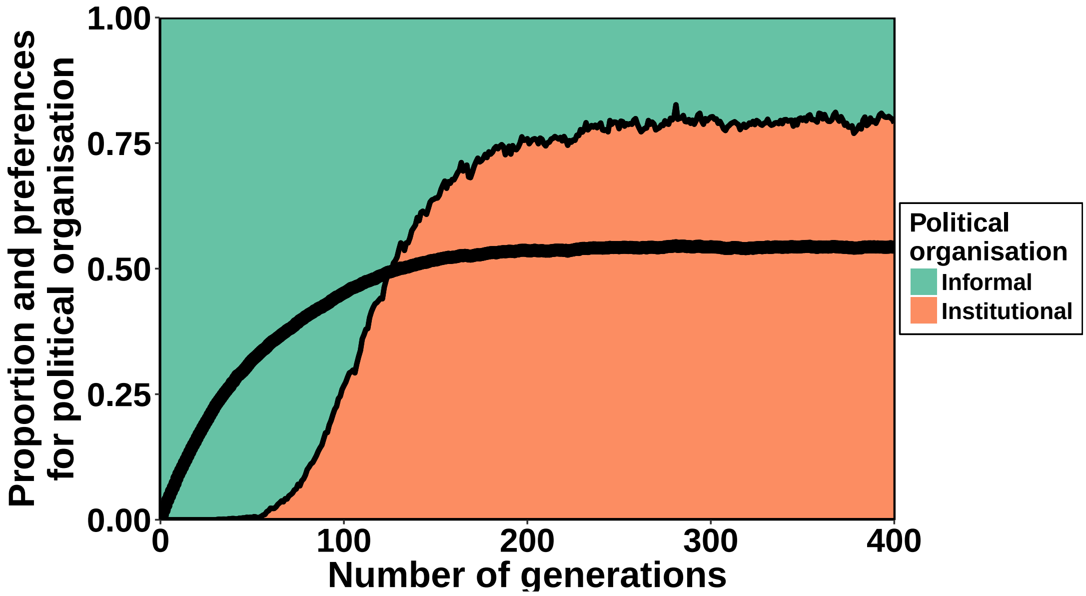

Figure 5.1: Evolution of the distribution of political organisation h^* (colour) and mean proportion of individuals with preferences towards institutional hierarchy as a function of generations. The values presented are the average across 32 replicates.

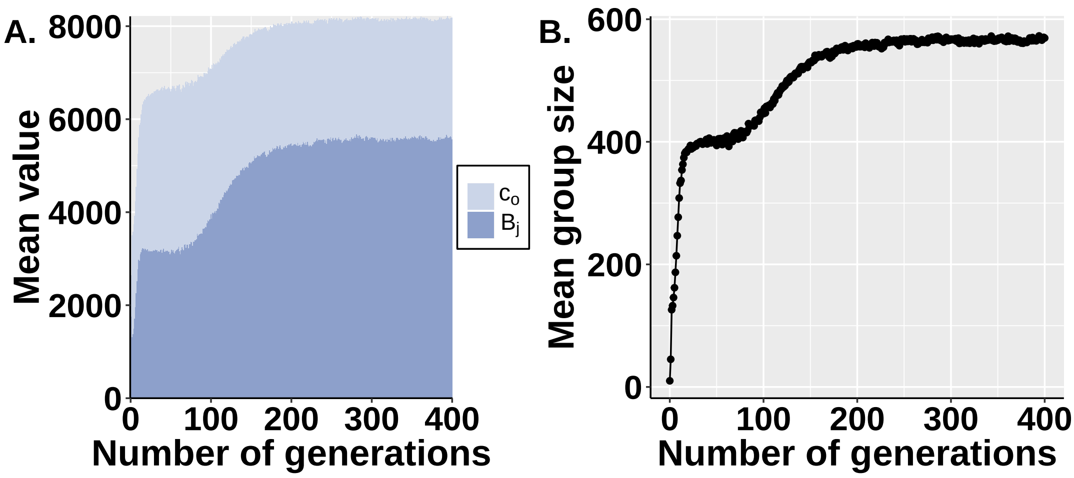

Figure 5.2: (A) Evolution of mean additional resources B (dark) equal to total resources produced discounted by cost of organisation C_o (light) across generations. (B) Evolution of mean group size across generations. The values presented are the average across 32 replicates.

Figure 5.1 demonstrates that for a moderate cost of institution, individual preferences evolve towards institutional hierarchy and thus, most of groups switch from informal to institutional hierarchy. Groups have in average only slightly more than 50% of individuals with preference toward institutional hierarchy because having any proportion above 50% has the same effect on political organisation and therefore the same effect on the fitness of all individuals within the group. The small proportion of groups with informal hierarchy are explained by the cost of the institution and random mutations in individual's preferences, which can lead some groups to temporarily switch

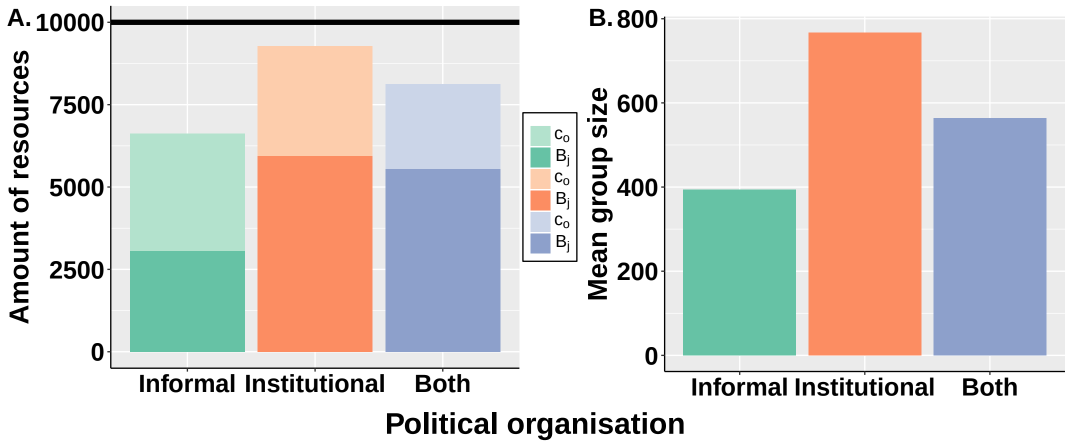

Figure 5.3: (A) mean additional resources B (dark) equal to total resources produced discounted by cost of organisation C_o (light), and (B) mean group size between simulations where are only allowed either institutional, informal or both organisations. The values presented are the average across 32 replicates.

back to informal hierarchy. The prevalence of institutional hierarchy remains stable for long period (5000 generations). Figure 5.2 shows that the total amount of resources produced and thus the group size increases through time. The cost of organisation also increases but remains low enough so that a large group provides more resources than a small group. Figure 5.2 shows that two increases in production and group size happen. The first corresponds to the emergence of informal hierarchy, and the second to the subsequent emergence of institutional hierarchy. This result and the results presented in Figure 5.3 demonstrate that institutional hierarchy allows a higher production and a larger group size. This is because a group with institutional hierarchy has (i) a lower cost of organisation (as seen in Chapter 3 single leader hierarchy has the shortest time to consensus) and, (ii) a larger production of surplus resources due to the larger size they reach. When both types of organisation are allowed, groups reach an intermediate size and productivity because of the cost of institution and the presence of a minority of small groups with informal hierarchy. To summarise, groups developing institutional hierarchy strongly reduce their cost of organisation. They grow larger, which improve their productivity, while hierarchy limits the increase in the cost of organisation. As a consequence, these groups export a greater number of migrants, who carry their cultural preferences for institutions to other groups, leading to the global spread of institutions.

Figure 5.4 shows that an increase in the cost of institution C_h reduces the proportion of institutional hierarchy and the average group size. This result is explained by the high cost of institution overcoming the benefit brought by institutional hierarchy. However, institutional hierarchy still evolves even for a moderate cost of institutions. Indeed, a cost of 1 means that all individuals within a group need a growth rate twice higher and thus, need to produce approximately twice as much resources to sustain the same fitness

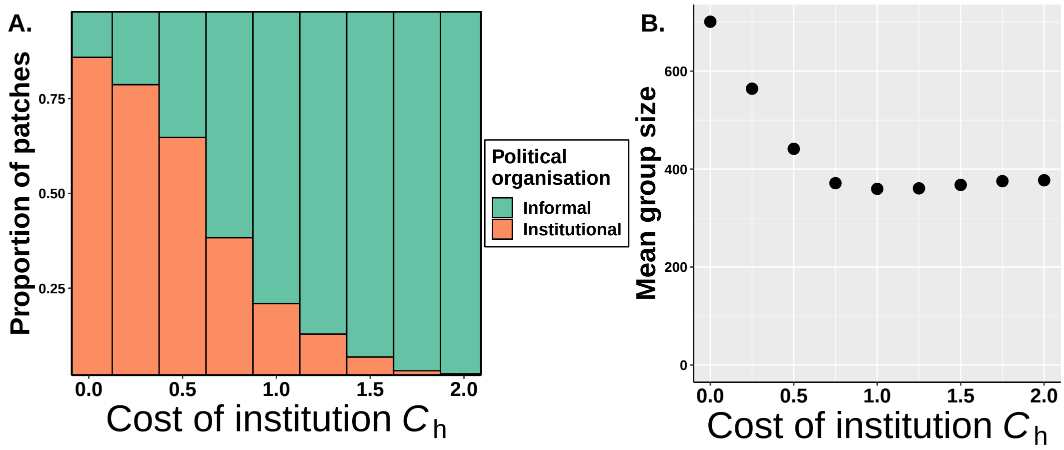

Figure 5.4: Distribution of (A) political organisation h^* and (B) mean group size as a function of the cost of an institution C_{h}. The values presented are the average across 32 replicates and 5000 generations.

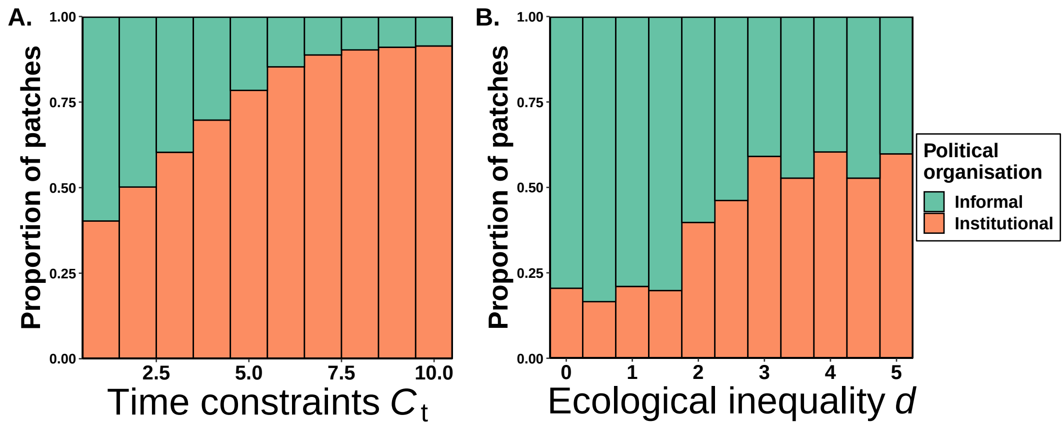

Figure 5.5: (A) Distribution of political organisation h^* as a function of time constraint C_{t}. (B) Distribution of political organisation h^* as a function of level of ecological inequality d with $C_{\text{h}} = 1$

. The values presented are the average across 32 replicates and 5000 generations.

(see equation 5.5). Moreover, Figure 5.4 shows that individuals develop institutional hierarchy even if it doesn't significantly modify the average group size, e.g. same size between $C_{\text{h}} = 1$ and $C_{\text{h}} = 2$. This is explained by single-leader hierarchy providing a more constant organisational benefit than the multiple leaders of informal hierarchy. Figure 5.5.A shows that a larger proportion of groups develop institutional hierarchy when the time constraints on the decision-making C_{t} is high, e.g. a time limited task such as warfare. This is because the shorter consensus time brought by single-leader hierarchy has more consequences on the absolute group production.

Figure 5.5.B shows that a higher proportion of groups develop institutional hierarchy when the level of ecological inequality d is higher. This result is explained by Figure 5.6 which shows that the benefit provided by institutional hierarchy persists even under

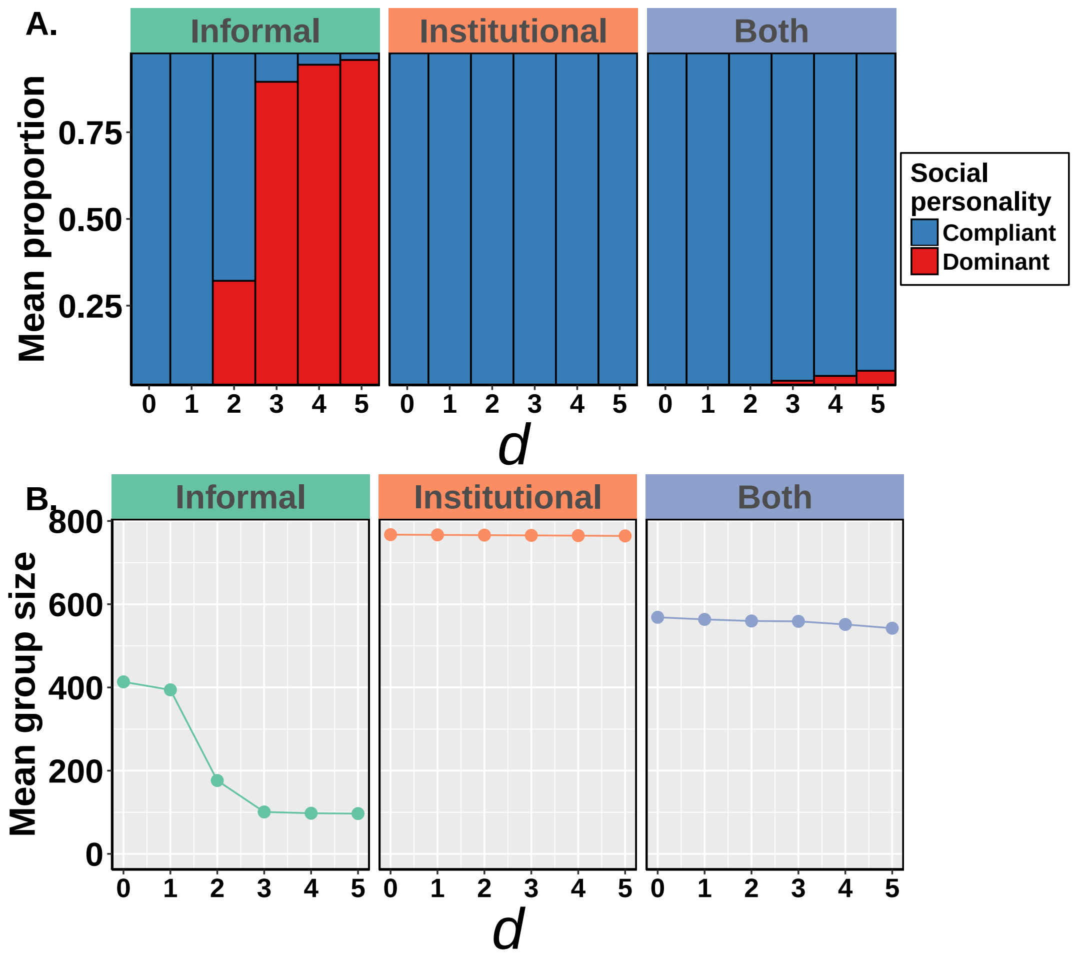

Figure 5.6: (A) Mean distribution of social personality and (B) mean group size as a function of the level of ecological inequality d. The values presented are the average across 32 replicates and 5000 generations.

high inequality. On the contrary, Figure 5.6.A shows that in an informal organisation, an increase in the level of inequality leads to an increase in the number of leaders. This results in a collapse of hierarchy, a high cost of organisation and smaller group size (Figure 5.6.B). This difference in the effect of inequality is explained by institutional hierarchy having only one expressed leader even if multiple individuals want to be leaders. In addition, only one individual attains the status of leader and hence receives a surplus of resources, which ultimately limits the increase in number of dominant individuals.

5.6 Discussion

Human social hierarchy can be formed because individuals act as leaders and followers, i.e. informal hierarchy, or because certain individuals are chosen as leaders and followers, i.e. institutional hierarchy. But why do human groups create costly institutional hierarchies if hierarchy already emerges naturally from individual behaviours? One key difference is that single leaders can appear in institutional hierarchy designed by group decision, but are highly unlikely in informal organisation shaped by evolution of personality traits. In Chapter 3, we have shown that institutional hierarchy with a single leader leads to bigger reductions in (i) the consensus time, (ii) the variation in the consensus time, and (iii) the increase in consensus time as a group grows. The evolutionary model developed here demonstrates that this difference results in the evolution of individuals' preferences toward institutional hierarchy, even if this has an additional cost.

Previous theoretical work have investigated the emergence of either informal or institutional hierarchy, but ignored the competition between the two forms. Powers and Lehmann (2014) developed an evolutionary model in which individuals favour institutional hierarchy over an egalitarian organisation. The model presented in chapter 4 has shown that a similar process can drive the evolution of individuals towards leader and follower behaviours, thus creating an informal hierarchy. We confirm and connect these works by showing that institutional hierarchy can be favoured over informal hierarchy because it provides additional benefit to group decision-making, in terms of consensus time.

Our model predicts that institutional hierarchy evolves when (i) group size is high (and so productivity and cost of organisation are high), and (ii) inequality is high. These predictions fit with the environmental and social changes observed following the advent of agriculture (Bocquet-Appel, 2011; Mattison et al., 2016). However, our model also predicts that the productivity benefit of institutional hierarchies can be counterbalanced by a high cost of institutions. It is hard to evaluate the costs implied by institutions, but it is worth noting that they result mostly from the resources and time allocated to monitor and punish individuals not complying with the rules, i.e. here individuals trying to become leaders. Our model has shown that institutional hierarchy limits the number of individuals aspiring to become leaders, and thus suggests that the costs of institutions remain limited even in large groups. Integrating the explicit process by which individuals are monitored and punished could give further insights.

It is worth noting that instead of competing, the two forms of political organisation could have interacted and even facilitated the development of each other. First, informal hierarchy could have facilitated the development of institutional hierarchy. On the one hand, the development of informal hierarchy creates favourable conditions for institutional hierarchy, i.e. higher group size and higher inequality. On the other hand, informal hierarchy could have provided enough influence to some individuals for them to convince the rest of the group to create institutional hierarchy. By doing so, they could have strengthen and legitimated their position. Such possibility could be explored by explicitly describing the collective decision-making by which the institution is created. Second, institutional hierarchy could have led to the development of informal hierarchy. Indeed, the influence of an individual is in truth defined by both an individual's personality and its social position. Thus, institutional hierarchy could have driven the evolution of few individuals toward a more extreme leader personality because it increases their chance to be chosen as leader or increases their efficiency as leader. Integrating a composite value of influence in this model could provide more insight into this interaction between these two forms of political organisation. In conclusion, these explanations for the emergence of institutional hierarchy are not mutually exclusive with the one presented here and if our results do not settle the question, they show that institutional hierarchy could have emerged first and indepently. Measuring the cost of organisation in informal and institutional hierarchy for instance in experiments, would help understand how critical and general is this explanation.

Importantly, stable single-leader hierarchy could theoretically exist in informal hierarchy if individuals have conditional behaviour, e.g. an individual choose to be follower if at least one individual is already a leader. However, it is unlikely in absence of institutions because it would require that an individual monitor and remember the behaviours of all other members of the group. Doing so would carry a high cognitive and time cost, in particular in large groups. Nonetheless, it could be made possible if leaders are heavily signaled and promoted. Further work on the evolution of conditional leader and follower would provide a crucial test to the presented explanation.

In this model, we have explored only one form of institution and one function of hierarchy. It would be interesting to explore other types of institutions, such as those allowing multiple levels of hierarchy, or restrict the number of people involved in the decision-making, as found in representative democracy. Other functions of hierarchy could also be investigated, e.g. to enforce cooperation (Hooper et al., 2010). However, it is worth noting that extending the model to integrate the possibility of voting for more leaders would carry similar qualitative results with individuals evolving a preference toward one leader. The presence of multiples leaders appears only later in human history, with the rise of complex states composed of multiple layers of hierarchy (Spencer, 1990).

We have considered only one form of group decision-making for choosing whether or not the group has institutional hierarchy, knowingly a majority rule. However, in real world, the decision for institutional hierarchy can be the result of more complex voting systems. Future work could investigate how different rules affect the emergence of institutional hierarchy. As a first step, the majority rule could be replaced by a sigmoid function which gives a probability of having institution as a function of the number of individuals with preferences toward institutional hierarchy. In this case, we would expect that the mean proportion of individuals with preferences towards institutional hierarchy evolve to a high value rather than remaining just above 0.5 as observed here.

Finally, we considered that the leader is chosen among individuals with dominant personality. Choosing the leader among any individuals (dominant and compliant) or choosing the leader following preset rules, e.g. heritable leadership, should remove the benefit of dominant personality in institutional hierarchy. This would reduce the proportion of dominant personalities. Ultimately, this could reduce the cost of institutional hierarchy because less individuals would need to be punished for not complying with their assigned roles of follower. Future work integrating explicitly the cost of institution i.e. monitoring and punishing, could provide a better insight in these situations. Such extension would be particularly relevant to explore the emergence of heritable leadership.

Institutions are believed to be crucial innovations for the emergence of human societies. We have shown here that one of their major benefit is to provide humans with a finer tool to modify their behaviour, which can be crucial for some processes such as shown here with hierarchy. More than a new innovation, the development of institutions marks a transition in the dynamics shaping human behaviours: from long and blind evolutionary process to fast cultural dynamics.

The first part of the "iron law of oligarchy" states that influential leaders and influeanceable followers will emerge to facilitate group organisation, as group grows. In this chapter and chapter4, we have shown that this explanation is a viable scenario, which fits with the evolution theory. The second part of the iron law of oligarchy proposes that once few individuals have a high influence, they can use this influence to bias opinions and impose inequality. We investigate this statement using an evolutionary point of view in the next Chapter 6.

Sixth Chapter

The evolution of despotism in hierarchical societies

In previous models of evolution of hierarchy (Chapter 4 and Chapter 5), social hierarchy creates inequality because influential leaders bias the decision and receive a higher share of resources. Yet this explanation is limited because leaders' behaviours are still constrained indirectly by the satisfaction of the rest of the group.

6.1 Contribution

In this Chapter 6, we demonstrate that leaders in hierarchical societies evolve despotic behaviour despite the control of followers. We show that a transition from equality to despotism will happen in presence of (i) highly influential individuals with a preferential access of resources; and (ii) weakly connected followers. We show that this is because influential leaders are able to bias followers opinion, thus jeopardising the followers' capacity to monitor and punish despotic leaders.

6.2 Publication

The majority of the work in this chapter has been published as:

- Cedric Perret, Simon T.Powers, Jeremy Pitt and Emma Hart, *Can justice be fair when it is blind? How social network structures can promote or prevent the evolution of despotism*, Proceedings of Artificial Life Conference 2018, MIT Press, 2018

6.3 Introduction

Hierarchical societies are defined by a skewed distribution of power but also resources. In human societies, leaders tend to evolve despotic behaviour where they exploit followers in order to increase their own fitness (Hayden and Villeneuve, 2010; Hayden, 2001; Betzig, 1982). Common explanations to explain the emergence of despotism emphasise the importance of transmissible surplus resources (Mattison et al., 2016), the capacity of followers to avoid domination, and the ability of leaders to impose domination (Johnstone, 2000; Summers, 2005). However, these factors are limited to explain the emergence of despotism in the first place because pre-Neolithic tribes had strong anti-authoritarian mechanisms, by which they had been able to avoid leaders' domination for long period (Boehm, 2001).

In the absence of means to build up economic or military power, leaders could have established their dominance by accumulating political power, i.e. influence over collective decisions (Michels, 1911). To cope with the complexity inherent to large-scale coordination, human societies tend to facilitate collective decision-making by switching to hierarchy with a minority of influential individuals, i.e. leaders, and a majority of influenceable individuals, i.e. followers. It has been suggested that the sole skewned distribution of political power, i.e. influence over collective decision, is enough to lead to inequality and despotism (Michels, 1911). This is because leaders might exert this influence to leverage institutional rules and bias collective decisions, and ultimately tilt the distribution of cost and benefits toward their own advantage. For instance, being the one deciding of the distribution of lands provides an easy way to appropriate the most productive lands for itself.

Using this bias on collective decisions, leaders would have been able to accumulate economic and military power, which can then be used to impose dominance on the rest of the groups. But although leaders have a huge influence on collective decisions in hierarchical societies, leaders' behaviours are still constrained indirectly by the satisfaction of the rest of the group. In particular, hierarchy first emerges in egalitarian tribes with strong anti-authoritarian mechanisms to control aspiring leaders (Boehm, 2001). It might have been difficult for an individual to accumulate economical power *via* its influence without being punished for doing so. In response to too despotic rules, followers can start a revolution to overthrow the leader. This form of justice, where individuals judge how institutions and decision-makers treat them, is defined as interactional justice (Schermerhorn, 2012), and is a common way in which individuals exert control over their institutions in human societies. Nevertheless, such control could have been limited because followers often lack direct knowledge of leaders' behaviours and decisions. To control leaders, followers judge decision-makers by the state of the laws and rules they manage. The flaw of this system is that the monitoring of leaders is dependent of individuals having an accurate knowledge of the state of the system. This knowledge is often incomplete because of the size and complexity of large human groups. In particular, individuals first need to make a self-assessment of how they are being treated, i.e. build their own opinion from their personal experiences; and then make a collective assessment about whether to try to induce change, i.e. aggregate the opinions of other individuals. On the one hand, this kind of opinion formation based on individual and social learning produces a global assessment of the current state of institutions. On the other hand, it is also susceptible to manipulation and false opinions. For instance, a leader could spread a view of the state of the system which is false but advantageous to himself.

We have shown in Chapter 3 that leaders' influence on decision can result from their influence on others' opinions. In addition, leaders are often surrounded by a clique – a limited number of highly influential individuals, such as a patriarchal clan in early agricultural societies (Kaplan et al., 2009) or key policy-makers in contemporaneous communities (Miller, 1958). By providing them with preferential access to resources, leaders can cause the clique to have a positive opinion, which they then spread throughout the group as a result of their high connectedness. The opinion of followers thus becomes biased by the clique, blinding them to the actual level of inequality. This blindness could eventually limit the control of followers on the leader's decisions. In recent work, Pitt (2017) modelled this process and has formally demonstrated that a centralised social network with a leader and a clique biases the transfer of knowledge, and ultimately leads to misconceptions on the current fairness level of the society. From this, it was predicted that an incomplete transfer of knowledge could blind the interactional justice of followers and could allow the evolution of despotic leaders. However, this prediction has remained untested so far.

To investigate this prediction, we build a model to simulate the evolution of despotism. Individuals are described by their preferences on the distribution of resources, and their opinions on the actual level of fairness in the society. We integrate the interactional justice process, i.e. self assessment and global assessment of leader's decision on the distribution of resources. Whether a leader remains in power is controlled by the overall satisfaction of group members, as determined by their joint assessment of leaders' behaviour. Opinions on leader's decisions are likely to be shaped by social links along a long period of time rather than in a short and disordered manner as seen in collective decision-making. Thus and to connect to previous work (Pitt, 2017), we describe social organisation of a group by its network structure, with hierarchy being described by a centralized network with the leader and its clique as the central node. We use a Moran process (Moran, 1958; Lieberman et al., 2005) to simulate the evolution of their distribution preferences [1] and investigate the following question:

Research question. *Does a centralised social network structure lead to the evolution of despotism in hierarchical societies ?*

[1] Moran process is a stochastic process that can be used to model evolution in finite population with overlapping generations. It describes a sequence of event, in which one individual is replaced by another individual. Fitness increases the probability of an individual to replace the dead individual. For more details, see (Moran, 1958; Otto and Day, 2007).

6.4 Model definition

To investigate the impact of social network structure on the evolution of despotism, we have developed a model to simulate the evolution of distribution preferences within a hierarchical society. This section provides an outline of the model with a detailed description of the mechanisms implemented: the network structure, the distribution of resources, the interactional justice and the reproduction.

6.4.1 Model outline and life cycle

We consider a fixed-size population of N individuals explicitly organised in a directed network. The population is composed of one leader deciding of the distribution of resources and $N-1$ followers. In addition, the population is divided between N_c highly influential individuals called clique members which includes the leader, and N_o individuals with low influence called outgroup members . The life cycle consists of:

1. The group produces an amount of resource that is distributed amongst group members according to the distribution preference of the leader, z_L (Equation 6.3).
2. Each individual builds its *own subjective mindset* about the fairness of resource allocation, m, as a function of the resources it personally received and its own distribution preference (Equation 6.4).
3. Each individual builds its *opinion* about the overall fairness of the resource distribution, o, by aggregating its own mindset and the mindsets of the neighbouring individuals (individuals linked to the focal individual) (Equation 6.5).
4. Each individual compares its *opinion* to its distribution preference z. If the opinion is higher than the preference, the individual is considered defiant and pays a cost to attempt a revolution.
5. In case of a large proportion of defiant individuals within the population, i.e. above a revolution threshold T, a new leader and clique are chosen within the defiant individuals. The network is then rebuilt.
6. A random individual dies and is replaced by another individual with a probability proportional to its fitness (Equation 6.1). This reproductive process is repeated R times.

Individuals are modelled by one cultural trait; their distribution preference z defined between equal ($z = 0$) and strongly skewed ($z = 1$). In leaders, this trait z_L is translated into the function defining the distribution of resources with $z_L = 0$ representing a fair leader and $z_L = 1$ a despotic leader. In followers, this trait is translated into their tolerance towards inequality, with the minimum $z = 0$ equal to no tolerance and the maximum $z = 1$ equal to the maximum tolerance where any level of despotism is accepted. The agents are also indirectly described by their influence α, here translated into the probability that the focal node is connected toward another individual. The trait z evolves following a Moran process (Moran, 1958; Lieberman et al., 2005). In addition, when a new individual is born, its trait z can mutate at a rate μ_z. When a mutation occurs, a random value is sampled from a truncated Gaussian distribution centered on the current value of the trait, with variance σ_z.

6.4.2 Network structures

To study how hierarchy can affect the evolution of despotism, we explicitly describe the social structure of the population by a directed social network. In this network, each node represents an individual and each directed link represents a social contact from one individual to another. We define the in-degree and the out-degree of an individual as the number of links connected respectively toward and from this focal node. The influence of an individual is taken to be its connectedness α defined as the probability of an individual to be connected toward another individual. To build the network, we use an algorithm derived from the Erdős–Rényi model (Erdős and Renyi, 1959) as follows:

1. The leader and all members of the clique are fully connected.

2. For each individual, a directed link is created from the individual i to the individual j following a probability α_c if the focal individual i is member of the clique or is the leader, and α_o if the focal individual i is a follower.

If a node is not connected to any individual at the end of the algorithm, one link is added from that node towards a randomly chosen individual. The network structure is then described by the value of α_c and α_o. We consider a network as random when $\alpha_c = \alpha_o$, and as centralised when $\alpha_c > \alpha_o$.

6.4.3 Reproduction

We consider here the evolutionary process as only cultural evolution (Boyd and Richerson, 1985). The evolution of the population is modelled by a Moran Process (Moran, 1958; Lieberman et al., 2005). This has been shown to be an efficient method to study evolution in finite populations and keeps the size of the population constant. The reproduction follows a death-birth process. At each time step, a randomly chosen individual dies. Then, the vacant node is replaced by the offspring of an individual chosen within the population with a probability proportional to its fitness, i.e. fitness-proportionate selection. The individual chosen to die is also competing to fill the vacant node with one of its own offspring. More formally, the new individual has a probability $P(i)$ to be the offspring of individual i according to :

$$P(i)(t) = \frac{w_i(t)}{\sum_{j=1}^{N} w_j(t)}, \tag{6.1}$$

with N the population size, w_i the fitness of an individual, and $j = 0$ the individual previously occupying the node. We assume that a vacant node can be replaced by any other individual in the population, i.e. the individual changing its distribution preference can learn from the observation of any other individual. Because we consider the opinion formation to happen on a longer time scale than the evolution of cultural items, this process is repeated R times by generation. The fitness is determinate by the distribution of resources.

6.4.4 Distribution of resources

At each round, the group produces a fixed amount of resources $B = 2N$. The resources are distributed as a function of the social position s_i of the individual, with the social position of the leader, clique and followers being respectively 0, 1 and 2. The fitness $w_i(t)$ of an individual i at a time t is equivalent to the resources received:

$$w_i(t) = B * f(s_i(t)) \tag{6.2}$$

The function defining the distribution $f(s_i(t))$ is modulated by the leader preference z_L such that :

$$f(s_i(t)) = \frac{e^{-s_i(t)*z_L(t)}}{\sum_{j=1}^{N} -e^{s_j(t)*z_L(t)}} \tag{6.3}$$

The distribution of resources is normalised and is bounded between an equal distribution of resources (with $z = 0$) and a strongly skewed distribution of resources (with $z = 1$). We make the assumption that the leader has full control on collective decision. This is a common assumption in the literature on the evolution of despotism (Buston et al., 2007).

6.4.5 Interactional justice

Each individual i has an opinion $o_i(t)$ describing its view of the current fairness of the society. It is the result of its own mindset $m_i(t)$, which is calculated from its own personal experience, and the mindset of its incoming social neighbours. First, an individual's mindset is calculated by comparing the resources it received with an egalitarian distribution:

$$m_i(t) = \frac{1/N - p(t)}{1/N - p_{min}} \tag{6.4}$$

The mindset is normalised by the difference between the maximum share $1/N$ and the minimum possible share p_{min}. As a result, the mindset is not dependant of the absolute amount of resources produced B. The opinion $o_i(t)$ of individual i is then calculated as:

(6.5) $$o_i(t) = \frac{m_i(t)L + \sum_{j=1}^{k} m_j(t)}{k_i(t) + L},$$

with j an incoming neighbour, $k_i(t)$ the in-degree of the focal node, and L a weight determining the relative importance of its own experience compared to the mindset of neighbours.

The variables m and o are bounded between 0 (totally satisfied) and 1 (totally dissatisfied). An individual is considered defiant if its opinion value is more than its tolerance threshold $z_i(t)$. A defiant individual then pays a cost to attempt a revolution C. In case of a large proportion of defiant individuals within the population, i.e. above a revolution threshold T, the current leader and clique become outgroup members and a new leader and clique are chosen from the defiant individuals. The network is then rebuilt.

6.5 Results

To provide a comprehensive investigation of our research question, we perform two analyses. In our first analysis, we consider that only the leader expresses its distribution preference z_L and that followers' distribution preference z_f is fixed. Then, we combine mathematical analysis and numerical simulations to study the effect of the network structure, e.g. α_c and α_o on the evolution of despotism. In our second analysis, we relax this assumption and use numerical simulations to allow both leader and follower preferences to evolve. We define the level of despotism as the level of inequality imposed by the leader which is here its distribution preference z_L.

6.5.1 Analysis 1: Evolution of despotism level with fixed followers' tolerance

We consider first that only the leader expresses z and that followers' distribution preference z_f is fixed. The fitness of the leader $w_L(t)$ is equal to:

(6.6) $$w_L(t) = \frac{1}{\sum_{i=1}^{N} - e^{s_i * z_L(t)}}.$$

It can be shown that the derivative of the fitness function $w_L(t)$ with respect to the level of despotism z_L:

(6.7) $$\frac{dw_L(t)}{dz_L} = \frac{\sum_{i=1}^{N} s_i e^{-s_i * z_L}}{(\sum_{i=1}^{N} e^{-s_i * z_L})^2} > 0$$

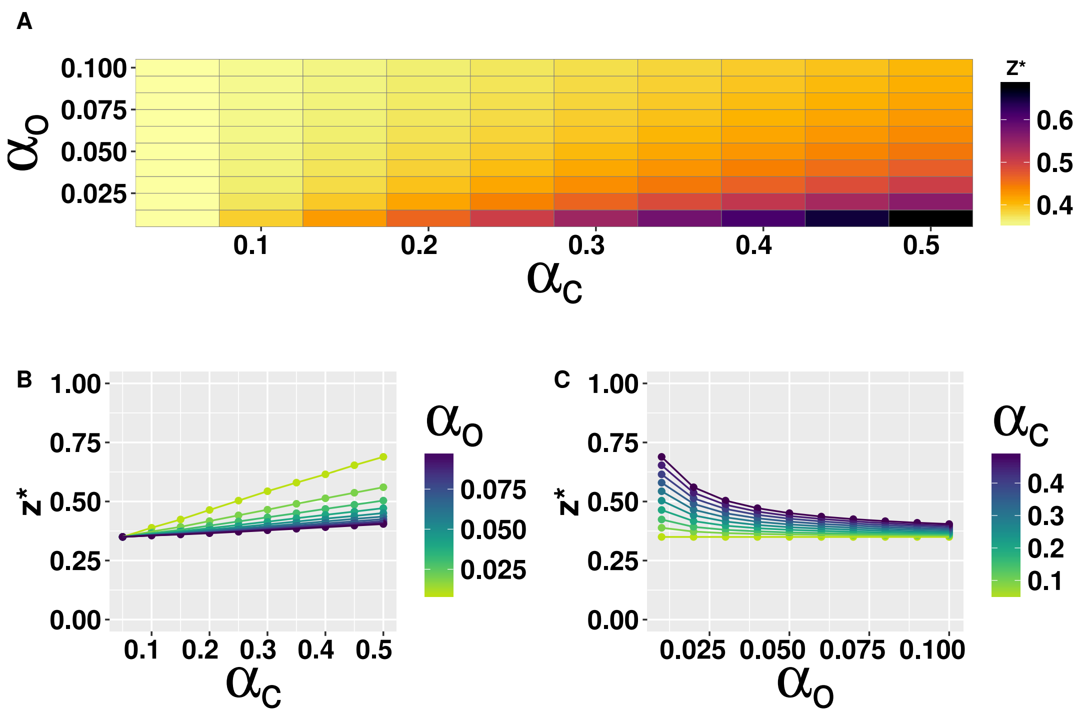

Figure 6.1: Mean value of the evolutionary stable point z^* in function of the connectedness of the clique α_c and connectedness of the outgroup α_o. The values presented are the average across 100 replicates.

In other words, an increase in the level of despotism z_L always increases the fitness of the leader and should be positively selected. However, it can exist a value z^* of the leader trait z_L between 0 and 1 for which the group undergoes a revolution. In this case, the leader becomes a follower and its trait z no longer affects the distribution of resources. When the tolerance of followers is fixed, the distribution of resources is the only selection pressure existing on z. Consequently, the level of despotism z_L will evolve towards the stable point z^* defined as the maximum value of z for which a revolution will not occur [2].

The value of this evolutionary stable point is a function of the network structure, i.e. α_c and α_o, for a given followers' tolerance and revolution threshold. Because it is not possible to analytically calculate z^*, we use numerical simulations to determinate its value as a function of α_c and α_o. The default parameters used in the simulations, unless otherwise specified, are $N = 500$, $N_c = 25$, $L = 1$, $T = 0.1$, $z_f = 0.25$, $R = 100$. For each set of parameters considered, 100 independent simulations have been realised. The results presented, unless otherwise specified, are the mean value of replicates.

Figure 6.1.A demonstrates that centralisation of the network structure leads to a higher level of despotism z^*. The greatest level of despotism $z^* = 0.71$ is obtained for

[2]Note that we do not consider indirect benefits here e.g. less inequality could benefit the leader by increasing the fitness of individuals related to the leader. This is because first we are looking to large groups in which indirect benefits are limited. And second, this should have limited effect on our results because increasing the amount of resources received by a related individual requires to reduce of the same amount the amount of resources kept by the leader.

the maximum α_c and minimum α_o; and the lowest level of despotism $z^* = 0.35$ is obtained for the minimum α_c and maximum α_o. To better understand the contribution of each variable, a statistical model has been built. To take in account the heteroskedacity inherent to the model, we built a mixed linear regression model with α_o as a random effect. It shows that α_c, α_o and their interaction have a significant effect on the level of despotism at equilibrium z^* (p-value < 0.001). Because the presence of significant interaction limits the interpretation of the statistical model, a graphical representation is presented in figure 6.1.B and figure 6.1.C. They show that α_c has a linear positive effect on the level of despotism while α_o has a exponential linear effect on the level of despotism. In addition, it also depicts a strong interaction between the two variables with the positive effect of α_c on despotism being strongly dependent of the value of α_o. In other words, a more centralised system lead to higher despotism only when followers are also disconnected from each other. Therefore, it suggests that increasing connectedness of outgroup members is a efficient way to limit the evolution of despotism.

6.5.2 Analysis 2: Evolution of despotism level and follower's tolerance

In our second analysis, we allow the tolerance of followers to evolve. Because of the complexity of the model, we use numerical simulations to analyse the model. The results of interest are the mean value of the distribution preference z and the level of despotism defined as the leader's value of distribution preference z_L. In addition, we present the mean value of mindset m obtained from self-assessment, the mean value of opinion o obtained from interaction with neighbours, the mean value of bias defined as the difference between m and o and the frequency of revolution events within the population. We present the average over long-run time over $5X10^7$ generations by sampling 50 data points every $1X10^6$ time steps. This method is confirmed as a good approximation of the stationary distribution by the absence of a periodic pattern of cycles and the standard error between simulations being always less than 0.027 . The default parameters used in the simulations, unless otherwise specified, are $N = 500$, $N_c = 25$, $L = 1$, $T = 0.1$, $R = 100$, $C = 0.1$, $\sigma_{\mathrm{m}} = 0.01$ and $\mu = 0.01$. The initial values of z are sampled on the uniform distribution between $[0, 1]$. For each set of parameters considered, 50 independent simulations have been realised. The box plots represents the dispersion of the mean value across time. The results presented as scatter plots show the mean value of replicates and the error bars represent the standard error between the mean value of replicates.

Figure 6.2 confirms that increasing the connectedness of the leader and its clique significantly leads to a higher level of despotism z_L, even when the distribution preference of followers also evolves. Figure 6.2 shows that above 0.1, further increasing the connectedness of the clique does not have a significant effect. However, this plateau is explained by the maximum limit imposed on the distribution preference z. As be-

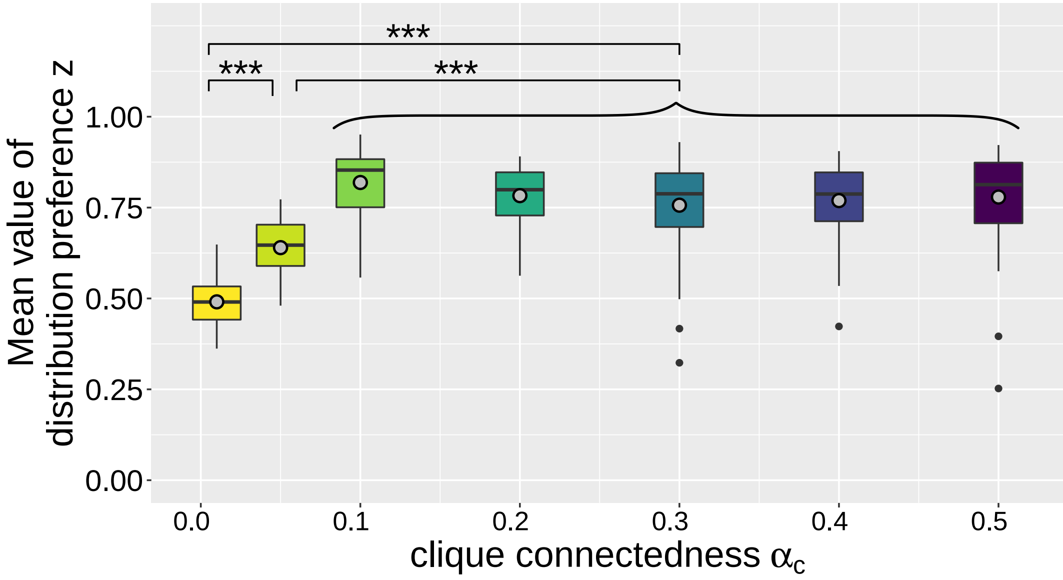

Figure 6.2: Long-run time averages over 5 X 10^7 generations and 50 replicates of the mean level of fairness z as a function of clique connectedness α_c. Grey circles represent the mean value of distribution preference of the leader z_L. Results are compared by pairwise Welch's t-test (***: p-value $< 1X10^{-6}$)

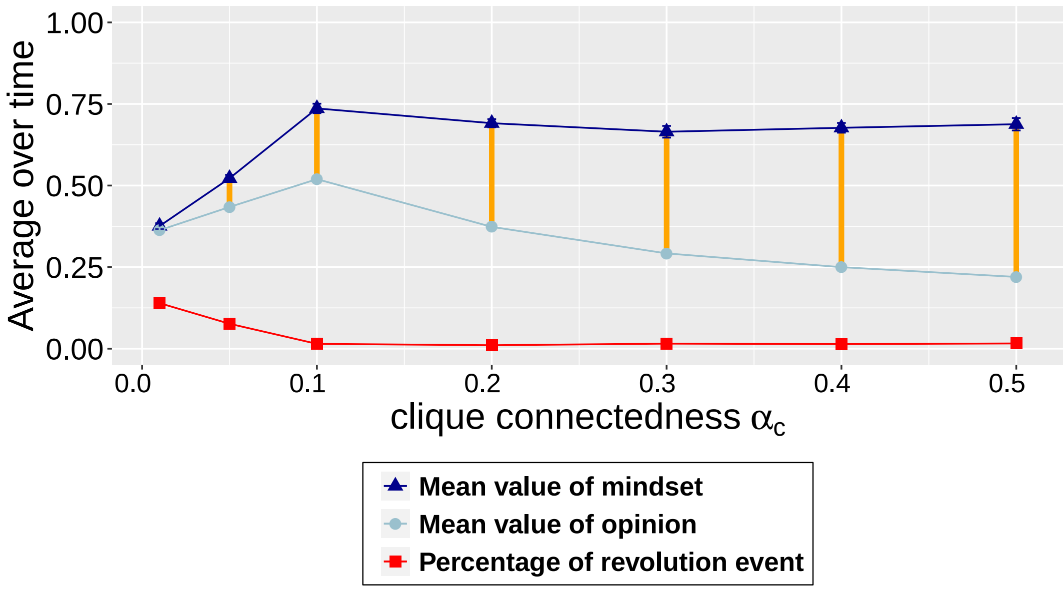

Figure 6.3: Long-run time averages over 5 X 10^7 generations and 50 replicates of the mean mindset m, mean opinion z and mean percentage of revolution as a function of clique connectedness α_c. Orange bars represent the mean value of bias defined as the difference between mindset and opinion.

fore, this result is explained by the evolution of leader distribution preference being controlled by the threshold at which followers start a revolution and change the leader and its clique. Figure 6.3 highlights the mechanism behind the centralisation effect: an increase in clique connectedness α_c is translated into a higher negative bias of opinions which leads to a lower frequency of revolution, and ultimately a higher mean level of despotism. In addition, Figure 6.2 demonstrates a similar positive effect of the con-

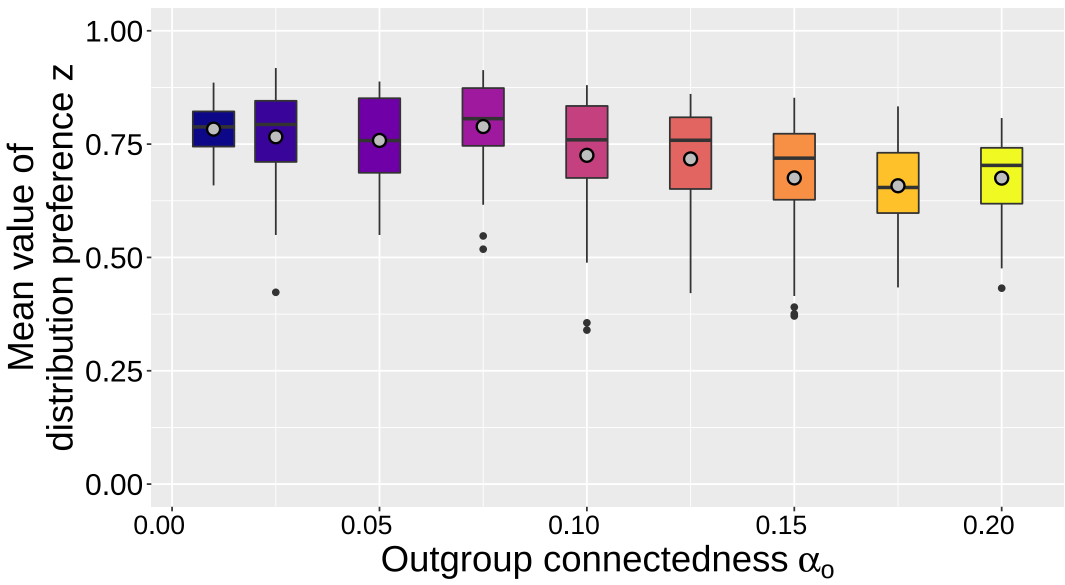

Figure 6.4: Long-run time averages over 5 X 10^7 generations and 50 replicates of the mean level of fairness z as a function of outgroup connectedness α_o. Grey circles represents the mean value of distribution preference of the leader z_L.

nectedness of the leader and its clique on the mean value of distribution preference z. In other words, centralisation leads followers to be more tolerant to despotism. By deciding of a more skewed distribution of resources, the leader increases its fitness which causes its distribution preference to spread in the population (the leader is more often copied). This effect associated with the cost of revolution leads to the mean value of distribution preference being close to the leader distribution preference. It is also worth noting that even in a random network and in absence of bias, followers evolve a relative tolerance to despotism. In addition, in contrast to the previous result, the model including the evolution of followers' preference has an overall higher level of despotism. This result is explained by the follower preference for equality being limited by the cost of revolution and the necessity of having a threshold proportion of individuals being in a defiant state at the same time. Finally, a close-up look at the simulations show that z strongly vary because of succession of period of increasing despotism and period of revolution. Indeed, the follower preference for equality is dependent of the leader preference and leads to chaotic variations. Despite this, the upper limit value of z and its average on long-run time confirms the positive effect of centralisation on the level of despotism.

Figure 6.4 shows that increasing the connectedness of followers leads to a lower level of despotism z_L, even when the distribution preference of followers also evolves. In addition, it demonstrates a similar effect on the mean value of distribution preference z for the reason stated previously. Both of these effects have been tested using a linear regression and are statistically significant (p-value < 1.10^{-6}). It is worth noting that the effect of the connectedness of followers on the level of despotism is smaller in

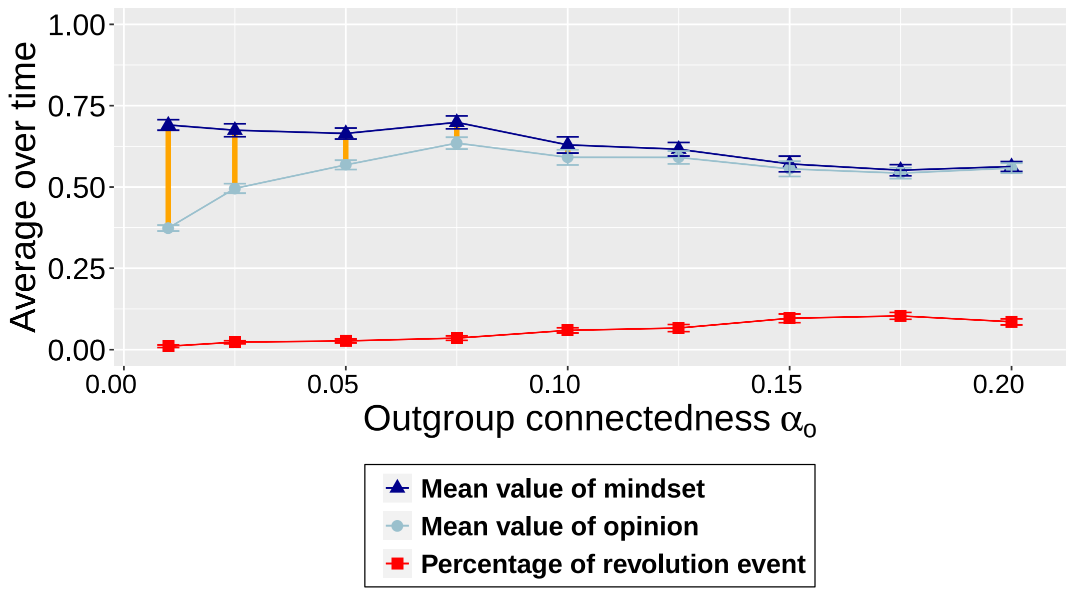

Figure 6.5: Long-run time averages over 5 X 10^7 generations and 50 replicates of the mean mindset, mean opinion z and mean percentage of revolution as a function of outgroup connectedness α_o. Orange bars represent the mean value of bias defined as the difference between mindset and opinion.

comparison to the results where the tolerance of followers is fixed. However, Figure 6.5 confirms that increasing the connectedness of followers greatly reduces the bias and therefore increases the frequency of revolution in response to despotic behaviour. In other words, the influence of the leader and its clique which blind followers judgement is dependent of disconnected followers. Therefore, the smaller effect of α_o on the level of despotism in this analysis is due to the other constraints affecting the cost and benefit of revolution as stated in the results looking at the effect of α_c . It suggests that the mechanisms by which individual organise a revolution also affects the evolution of despotism.

6.6 Discussion

Despite the potential benefits of the hierarchy, centralisation of decision-making appears to go along with despotism, i.e. inequality enforced by leaders. Yet, it is still hard to determine if inequality and despotism are an inherent consequence of centralisation or the result of a common element, e.g. agriculture. Although different factors have been identified, the role of distribution of influence and its impact on knowledge transfer has not yet been investigated. To fill this gap, we have simulated such a scenario by modelling the evolution of distribution preference in groups structured in different social networks. The model developed demonstrates that the centralisation of social networks leads to the evolution of higher despotism and inequality. In other words, a skewed distribution of influence is sufficient to create inequality. This result holds when the tolerance of followers is fixed or in a more realistic set-up where tolerance of followers evolve. This result is explained by the knowledge of followers on the leader's decision which is (i) biased by the influential members of the clique, and (ii) limited by their low connectedness to other followers. As a consequence, followers can not impartially enforce their control on leaders and *a fortiori* on collectively decided institutional rules. Furthermore, the model demonstrates that the effect of influential members on followers' opinion is strongly dependent on followers having low connectedness. Indeed, a slight increase in the influence of followers greatly reduces the despotism created by the clique influence. However, as shown by comparing the first and second analysis, this effect is weaker when follower's distribution preference is also evolving. Overall, this result suggests that increasing the connection between followers could be a solution to limit despotism in social systems.

The results presented here attempt to bridge the gap between two main research axes. Previous research work has either examined the impact of centralisation on opinion formation processes, but without evolutionary processes, or has studied the evolution of despotism without integrating mechanisms underlying opinion formation. On the former side, Gavrilets et al. (2016) show that the presence of highly influential individuals can strongly bias the collective decision. Later on, Pitt (2017) has integrated institutional rules and interactional justice into a multi-agent systems and show that hierarchy can bias the followers' opinion on leader decided rules. We here confirm that this result still holds even when the evolution of individual preferences for the distribution of resources are taken in account. Furthermore, we have shown that integrating the evolution of followers' preferences can lead to irregular level of despotism but yet, with the same qualitative behaviours as when only the leader's distribution preference evolves. On the other hand, reproductive skew theory used mathematical models to understand how the conflict between leader and follower affects the evolution of despotism (Summers, 2005; Johnstone, 2000). These models have identified the important factors behind the evolution of inequality such as the cost of leaving the group or the relative cost of conflict with the leader. Our results complete this previous work by integrating an opinion formation process and by identifying a new crucial factor in the evolution of inequality: the distribution of influence itself as modelled by social network structure. This factor has the advantage of explaining the rise of inequality from economically egalitarian groups.

Our model predicts that the capacity of followers to efficiently control leader's decision is crucial to limit despotism. This result is supported by evidence from behavioural economics experiments. In particular, two economics games called the ultimatum and the dictator game implement a similar version of the presented model. In the ultimatum game, one of two players has to decide how to split a fixed amount of money and the second player can choose to either accept it and both receive their shares; or refuse it in which case neither receive anything. However, in the variant called dictator game, the second player can't decide to accept or refuse. Experimental results show that in the ultimatum game, the proposer keeps in average 60% of the total amount while in the dictator game the share kept by the proposer goes up to 72% (Oosterbeek et al., 2004; Engel, 2010). In conclusion, the ability of followers to punish the leader reduces its tendency toward despotism. Importantly, our results predict that centralisation of the social network can blind the judgement of followers and transform the distribution of resources from an ultimatum game to a dictator game. Controlled experiments implementing these games in large groups could provide a first test to this prediction.

We made a number of assumptions to keep our model tractable. First of all, the model developed considers only blind evolutionary processes as a driver of change in distribution preferences. However, cognitive processes might also affect the evolution of agent preferences and lead to a lower level of despotism, e.g. followers predict that a low level of despotism favour their positions. This difference suggests that integrating cognitive processes might be crucial to limit despotism in social systems and would be worth investigating. Yet, it is important to note that our results still hold over large time scales in which evolutionary processes are a good predictor of cultural change (Boyd and Richerson, 1985). Another assumption made concerns the division of the society into only three groups and with only one leader. In natural social systems, hierarchy can be composed of many more layers. But this is unlikely to change our qualitative results since the results presented are explained by the asymmetrical distribution of influence. Nonetheless, it is crucial to explore similarly the evolution of despotism in other hierarchical network structures. Finally, we have considered here a simplified version of the revolution process, which is a step function of the number of defiant individuals. This assumption leads to follower's connectedness having a limited effect on the evolution of despotism because it is difficult for followers to reach the minimum threshold required to do a revolution. This effect is similar to the result of Weingast (1997) who used a game theory model to show that revolution is itself a costly coordination task and that revolution could be successful only in limited conditions. It is important to extend the model to consider different formalisation of revolution. For instance, extensions could consider that the probability of revolution is a gradual function of the number of deviants individuals, rather than a step threshold. Another possibility is that this limit induced by the threshold could be an important feature and the model could be extended to integrate the strategies used by individuals to respond to it. This could be done by integrating more explicitly revolution , e.g. as a Volunteer's Dilemma game, along with the strategies used by individuals to play this game.

In conclusion, this model sheds light on the importance of looking at distribution of influence as a critical factor to understand the evolution of despotism in human societies. This model combined with previous Chapter 4 and 5 provide a complete scenario to explain the transition from egalitarian groups to both functional and coercive hierarchical societies. It shows that "the iron law of oligarchy" theory and the scenario it proposes for the emergence of hierarchy is explainable in terms of evolutionary theory.

Seventh Chapter

Conclusion

The Neolithic transition marks a major turning point in human social organisation. In a few thousands years, humans groups switch from small tribes of egalitarian hunter-gatherer to large societies of hierarchical agriculturists. Yet, there is still a debate on the factors and mechanisms driving this transition. In particular, the evolution of exploited followers appears as an evolutionary paradox. In this thesis, we explore a theory from political sciences called "the iron law of oligarchy" using evolution as a new perspective. The iron law of oligarchy proposes that groups delegate power to a handful of individuals when group size increases. This is because a growth in group size increases the number and the complexity of decisions that a group needs to take in order to work collectively. Centralising authority would appear as a response to this scalar stress because it facilitates group organisation. The iron law of oligarchy states that once some individual possess a disproportionate political power, they can use it to bias group decision and individual opinions in order to create despotism and inequality. Despite this theory being supported by real world observations, this theory lacks of a more formal investigation. In particular, it did not consider the rules of evolution, despite hierarchy emerging from human behaviours and culture, both products of evolution.

In this thesis, we proposed the evolutionary iron law of oligarchy, which presents a formal model of the iron law of oligarchy, based on a well-accepted body of theory, the theory of evolution. We represented individuals by their capacity to influence collective decisions and social hierarchy as a skewed distribution of this influence. We have investigated the "evolutionary iron law of oligarchy" by combining models of social dynamics and evolutionary dynamics. We have filled multiple gaps and shown that:

- a skewness in individual's influence reduces the time that a group spends to reach consensus and thus can explain the benefit of hierarchy on organisation
- the organisational benefit of social hierarchy can lead to the evolution of leaders' and followers' behaviours, even if it creates inequality
- institutional hierarchy — by group decision — can outcompete informal hierarchy

— leaders and followers behaviours — despite its additional cost because hierarchy with a single influential leader provides a better organisational advantage.

- centralised network structure in hierarchical groups leads to the evolution of despotic leader because well-connected leaders can bias the opinions of isolated followers.

Overall, this thesis demonstrates that the evolutionary iron law of oligarchy is a viable scenario to explain the emergence of beneficial hierarchy and despotism in human societies. In other words, the demographic expansion that came along the advent of agriculture and its effect on group organisation is sufficient to explain the emergence of leaders and despots. On the one hand, this thesis contributes to evolutionary theories of the emergence of hierarchy by unifying voluntary and coercive theories. On the other hand, this thesis contributes to the iron law of oligarchy by identifying a set of conditions necessary for the iron law to apply. Ultimately, this thesis shows that the iron law of oligarchy fits within the paradigm of evolution theory and can be seen as a consequence of the law of evolution by natural selection.

In this thesis, we have focused on the emergence of hierarchy during the Neolithic transition. This is because the Neolithic transition is one of the most documented events and hierarchies observed after the Neolithic transition are relatively simple compared to more modern societies. However, the iron law of oligarchy originally proposed by Michels (1911) was built on and for modern organisations such as political parties. We believe that the evolutionary iron law of oligarchy developed here can also apply to these cases. Indeed, evolutionary processes encompass cultural items and preferences, which evolve in a short time scale. In addition, we have used here an abstracted approach which allows general conclusions. In other words, if the conditions and mechanisms considered in the model are present, then the results of the model hold and such, independently of the time period. For instance, an increase in group size can be due to a higher number of births or the recruitment of more individuals within a company. Yet, they are the same in abstract, in the sense that they would still result in an increase of the cost of organisation. Naturally, other mechanisms and processes might also take place in modern societies. For instance, large groups with participatory democracy can maintain egalitarian organisation even at large-scale. But rather than ignoring these cases, an abstracted model provides a mean to understand the effects of these additional mechanisms. On the same example, participatory democracy could be seen as reducing the increase of cost of organisation due to increase in group size and thus in the models developed in this thesis should lead to large but egalitarian groups.

Can the evolutionary iron law of oligarchy explain the emergence of more complex forms of hierarchy? In particular, chiefdoms are followed by the emergence of states, characterised by a multi layered and institutionalised hierarchy (Spencer, 1990). This question remains hard to answer. On the one hand, multi-layered hierarchy could be seen as a repetition of simpler forms of hierarchy, also driven by the same constraints on collective decision-making. In this case, the models developed here could be easily extended to explain the emergence of states. On the other hand, states could have qualitative differences and their emergence could be driven by different dynamics. Nonetheless, we have shown in this thesis the transition from an egalitarian group to the premises of states, institutional hierarchy.

The limits and further work related to each model is described in each contributed section. To summarise, they consist of two main aspects. First, the predictions of the models should be tested either using some real-world data or laboratory experiments. To do so, there is a large amount of data from anthropological studies which brought together can show trends (for global data Turchin et al. 2015; Garfield et al. 2019a) but also, new data are made available by the development of online experiments and online communities in which thousands of individuals coordinate and organise. Second, the models developed here can be extended. We remind here one major extension for each model. The opinion formation model presented in Chapter 3 can be extended to consider different update rules and an explicit network structure. This would provide insights on the generality of the benefit of a skewed distribution of influence on time to consensus. The evolutionary model of Chapter 4 can be combined with Chapter 6 to incorporate the evolution of despotic preferences. This would create a comprehensive model of the evolutionary iron law of oligarchy, which would simulate the evolution of both functional hierarchy and despotism. The model of Chapter 5 can be extended to include a value of influence defined by both personalities and institutions, in order to investigate the interactions between informal and institutional hierarchy. The model of Chapter 6 can be extended to integrate the strategies that followers use to efficiently coordinate during revolution, and thus provide more realistic predictions on the effect of social network structure on the level of despotism.

For simplicity, the models presented overlook the determinism of the traits studied and we considered that traits could be cultural or biological as long as they are vertically transmitted. In future work and when more data on the determinism of the traits studied will be available, it is important to extend our models to confirm the generality of our conclusions. For instance, traits with an important biological basis require models which integrate more biologically realistic assumptions such as sexual reproduction, diploidy and possibly multi-locus traits (Crow and Kimura, 1970). An important cultural basis of traits would call for extensions of the models which integrate horizontal transmission and particular forms of social learning such as conformity bias (Boyd and Richerson, 1985).
In this thesis, we have shown that describing the evolution of traits affecting the in-

fluence of individuals on others and on collective decision is sufficient to explain the emergence of helpful and despotic leaders. This abstract representation of leaders and followers, rather than a loss of details, identify the key features of leaders and followers. In addition, this abstraction has the benefit of generalising the results. For instance, the results presented in thesis could apply to living organisms doing collective decision-making by consensus (Conradt and Roper, 2005) and in which, some individuals are better at transmitting their preferences. This could apply to buffalos (Prins, 1996), African wild dogs (*Lycaon pictus*) (Walker et al., 2017) or bacteria doing quorum sensing (Miller and Bassler, 2001). Moreover, this formalisation of leaders and followers also provides a new approach for experimental work. Indeed, experiments working on hierarchy often rely on groups with explicitly elected leaders but ignore informal leadership. The models presented in this thesis do predictions on the influence of individuals, which is a characteristic that can be measured either from an individual's skills to communicate (if looking at intrinsic influence) or the distance between an individual initial preference and the final decision (if looking at realised influence).

More broadly, the work presented in this thesis fits within the field of social evolution, which aims to understand how evolution shapes social behaviours. The study of large-scale societies is a particularly thrilling topic in social evolution because large-scale human societies exhibit cooperation and coordination at an unprecedented scale. Yet, most of known mechanisms to ensure cooperation and coordination break down in large groups (Powers and Lehmann, 2017). This interest is illustrated by the shift from group to society sometimes described as the fifth major transition of evolution (Szathmáry and Smith, 1995; Szathmáry, 2015). We have explored here one feature of large-scale societies, hierarchy, and how it could explain coordination at large-scale. Another feature of large-scale societies is the prevalence of institutions which could explain the persistence of cooperation in large-scale (Ostrom, 1990; Powers et al., 2016). Interestingly, hierarchy and institution could have strongly interacted. First, it could be because hierarchy can be an institution as seen in Chapter 5. Second, it could be because institutional rules result from collective decision-making, which is a process strongly affected by hierarchy as we have seen in this thesis. Further work could focus on the effect of hierarchy on the final decision rather than the time to consensus, to look how the distribution of power could affect the evolution of institutional rules.

Despite the importance of understanding large-scale societies, their study has often been limited by the division of the topic between disciplines. In this thesis, we have proposed one interdisciplinary approach by combining models of social dynamics and evolutionary dynamics. We have shown that each field is able to fill gaps in the other field and ultimately, provide new perspectives. We believe that further work between these fields can be useful for understanding the emergence of human complex societies. For example, if statistical physics can provide a mathematical approximation of how the distribution of influence affects the time to consensus, this function could be integrated into more formal evolutionary model, e.g. kin selection model (Gardner et al., 2011) to provide a more general and robust analysis. Another example is that opinion formation models could be used to describe other phenomena, such as conflict resolution, in which leaders appear to play an important role (Glowacki and Rueden, 2015).

Finally, this thesis seems to draw a dark picture. Are humans condemned to despotism? This was the initial vision of Michels (1911) when writing its "iron law of oligarchy'. From his point of view, human groups will inevitably fall into an oligarchic organisation. Yet, as observed in the later criticisms of the iron law of oligarchy, despotism is not a certainty and egalitarianism can be maintained. Rather than supporting the "iron" part of the theory, this thesis provides means to avoid it by identifying the conditions under which oligarchy emerges — conditions which can be modified to maintain egalitarian organisation. For instance, the relationship between group size and cost of organisation can be reduced by other means that concentrating power in the hands of few. In particular, the development of internet allows discussion and coordination on a large scale for low costs. Another example is the relationship between inequality of power and despotism which can be limited by particular mechanisms. Constitutions are rules which clearly state the limit of power of leaders and make them accountable to the majority (Weingast, 1997). In truth, understanding the factors driving the emergence of hierarchy and despotism will open new perspectives to design better form of governance and management. Applications are not restrained to human societies. Artificial social systems share similar features to human groups. On the one hand, swarms of robots or smart grids connecting houses also need to coordinate with each other and at a speed that limits the intervention of humans. On the other hand, most multi agent systems can share similar capacities than humans, e.g. communication, memory. Already, knowledge on leadership and hierarchy is used to improve artificial social systems (Pugliese et al., 2015; Chih-Han et al., 2010). Ultimately, understanding the drivers behind social organisation could contribute to design better forms of governance for both artificial and natural societies.

Bibliography

Aimé, Carla and Frederic Austerlitz (2017). “Different kinds of genetic markers permit inference of Paleolithic and Neolithic expansions in humans”. In: *European Journal of Human Genetics* 25.3, pp. 360–365.

Alberti, Gianmarco (2014). “Modeling group size and scalar stress by logistic regression from an archaeological perspective”. In: *PLOS ONE* 9.3. Ed. by Angel Sánchez, e91510.

Alexander, R D (1974). “The evolution of social behavior”. In: *Annual Review of Ecology and Systematics* 5.1, pp. 325–383.

Allen, Robert C (1997). “Agriculture and the origins of the state in ancient Egypt”. In: *Explorations in Economic History* 34.2, pp. 135–154.

Alvard, Michael S. and Allen Gillespie (2004). “Good lamalera whale hunters accrue reproductive benefits”. In: Emerald Group Publishing Limited, pp. 225–247.

Alvard, Michael S. and David A. Nolin (2002). “Rousseau’s whale hunt?” In: *Current Anthropology* 43.4, pp. 533–559.

Ames, Kenneth M. (2003). “The Northwest Coast”. In: *Evolutionary Anthropology* 12.1, pp. 19–33.

Arnold, Jeanne E. (1993). “Labor and the rise of complex hunter-gatherers”. In: *Journal of Anthropological Archaeology* 12.1, pp. 75–119.

Arnold, Jeanne E. (2010). “The role of politically charged property in the appearance of institutionalized leadership: A view of the North American Pacific coast”. In: *The evolution of leadership : transitions in decision making from small-scale to middle-range societies.* 1st ed. Santa Fe, N.M. : School for Advanced Research Press, chap. 6.

Barnard, C.J. and R.M. Sibly (1981). “Producers and scroungers: A general model and its application to captive flocks of house sparrows”. In: *Animal Behaviour* 29.2, pp. 543–550.

Bass, Bernard M. (1990). “From transactional to transformational leadership: Learning to share the vision”. In: *Organizational Dynamics* 18.3, pp. 19–31.

Baumard, Nicolas (2010). “Has punishment played a role in the evolution of cooperation? A critical review”. In: *Mind & Society* 9.2, pp. 171–192.

Baxter, G. J., R. A. Blythe and A. J. McKane (2008). “Fixation and consensus times on a network: A unified approach”. In: *Physical Review Letters* 101.25.

Baxter, Gareth J., Richard A. Blythe and Alan J. McKane (2012). “Fast fixation with a generic network structure”. In: *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* 86.3.

Berggren, Niclas, Henrik Jordahl and Panu Poutvaara (2010). “The looks of a winner: Beauty, gender and electoral success”. In: *Journal of public economics* 94.1-2.

Berwick, Robert C. and Noam Chomsky (2016). *Why only us : language and evolution*, p. 215.

Betzig, Laura (1993). “Sex, succession, and stratification in the first six civilizations: How powerful men reproduced, passed power on to their sons, and used power to defend their wealth, women, and children”. In: *Social Stratification and Socioeconomic Inequality*. Ed. by Lee Ellis. New York: Praeger, pp. 37–74.

Betzig, L.L. (1982). “Despotism and differential reproduction: A cross-cultural correlation of conflict asymmetry, hierarchy, and degree of polygyny”. In: *Ethology and Sociobiology* 3.4, pp. 209–221.

Bingham, Paul M. (1999). *Human uniqueness: A general theory*.

Blythe, R. A. (2010). “Ordering in voter models on networks: Exact reduction to a single-coordinate diffusion”. In: *Journal of Physics A: Mathematical and Theoretical* 43.38.

Bocquet-Appel, J.-P. (2011). “When the world’s population took off: the springboard of the neolithic demographic transition”. In: *Science* 333.6042, pp. 560–561.

Boehm, Christopher (2001). *Hierarchy in the forest: The evolution of egalitarian behavior*. Cambridge: Harvard University Press.

Boone, James L. (1992). “Competition, conflict, and the development of social hierarchies”. In: *Evolutionary ecology and human behavior*. New York: Aldine de Gruyter, pp. 301–337.

Bowles, Samuel (2011). “Cultivation of cereals by the first farmers was not more productive than foraging”. In: *PNAS* 108.12, pp. 4760–4765.

Bowles, Samuel, Eric Alden Smith and Monique Borgerhoff Mulder (2010). “The emergence and persistence of inequality in premodern societies”. In: *Current Anthropology* 51.1.

Boyd, Robert and Peter J. Richerson (1985). *Culture and the evolutionary process*. University of Chicago Press.

Boyd, Robert and Peter J. Richerson (1992). “Punishment allows the evolution of cooperation (or anything else) in sizable groups”. In: *Ethology and Sociobiology* 13.3, pp. 171–195.

Breines, Wini (1980). “Community and organization: The new left and Michels’ “iron law of oligarchy””. In: *Social Problems* 27.4, pp. 419–429.

Briggs, Jean L. (1971). *Never in anger*. Ed. by Harvard University Press, p. 379.

Brown, Jerram L (1964). “The evolution of diversity in avian territorial systems”. In: *Wilson Bulletin* 76.2, pp. 60–169.

Bukharin, Nikolai. (1925). *Historical materialism : a system of sociology*. New York: International publishers.

Buston, P. M. and A. G. Zink (2009). “Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models”. In: *Behavioral Ecology* 20.3, pp. 672–684.

Buston, P.M., H.K. Reeve, M.A. Cant, S.L. Vehrencamp and S.T. Emlen (2007). “Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models”. In: *Animal Behaviour* 74.6, pp. 1643–1654.

Calvert, Randall (1992). “Leadership and its basis in problems of social coordination”. In: *International Political Science Review* 13.1, pp. 7–24.

Cant, Michael A (1998). “A model for the evolution of reproductive skew without reproductive suppression”. In: *Anim. Behav* 55, pp. 163–169.

Carneiro, Robert L. (1967). “On the relationship between size of population and complexity of social organization”. In: *Southwestern Journal of Anthropology* 23.3, pp. 234–243.

Carneiro, Robert L. (1970). “A theory of the origin of the state”. In: *Science* 169, pp. 733–738.

Casimir, Michael J. and Aparna Rao (1995). “Prestige, possessions, and progeny”. In: *Human Nature* 6.3, pp. 241–272.

Castellano, Claudio, Santo Fortunato and Vittorio Loreto (2009). “Statistical physics of social dynamics”. In: *Reviews of Modern Physics* 81.2, pp. 591–646.

Cavalli-Sforza, L L, M W Feldman, K H Chen and S M Dornbusch (1982). “Theory and observation in cultural transmission”. In: *Science (New York, N.Y.)* 218.4567, pp. 19–27.

Chabot-Hanowell, Benjamin and Eric Alden Smith (2012). “5 territorial and nonterritorial routes to power: Reconciling evolutionary ecological, social agency, and historicist approaches”. In: *Archeological Papers of the American Anthropological Association* 22.1, pp. 72–86.

Chapais, Bernard (2018). “From chimpanzee society to human society: bridging the kinship gap”. In: *Chimpanzees and Human Evolution*, pp. 427–463.

Chih-Han, Yu, Justin K. Werfel and Radhika Nagpal (2010). “Collective decision-making in multi-agent systems by implicit leadership”. In: *Proceedings of the 9th International Conference on Autonomous Agents and Multiagents Systems*. Association for Computing Machinery Press.

Claidiere, N., T. C. Scott-Phillips and D. Sperber (2014). “How Darwinian is cultural evolution?” In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 369.1642, pp. 20130368–20130368.

Claidière, Nicolas (2009). "Théories darwiniennes de l'évolution culturelle : modèles et mécanismes". PhD thesis. Université Pierre et Marie Curie, p. 368.

Clarke, Harold D., Matthew J. Goodwin and Paul Whiteley (2017). *Brexit: Why Britain voted to leave the European Union*, p. 256.

Clifford, Peter and Aidan Sudbury (1973). *A model for spatial conflict*. Tech. rep. 3, p. 881.

Cohen, Mark Nathan and Gillian Margaret Mountford Crane-Kramer, eds. (2007). *Ancient health : skeletal indicators of agricultural and economic intensification*. Gainesville (FL): University Press of Florida, p. 432.

Conradt, Larissa and Christian List (2009). "Group decisions in humans and animals: a survey". In: *Philosophical transactions of the Royal Society B: Biological Sciences* 364.1518, pp. 719–42.

Conradt, Larissa and Timothy J. Roper (2005). "Consensus decision making in animals". In: *Trends in Ecology & Evolution* 20.8, pp. 449–456.

Cooper, Russell W. (1999). *Coordination games : complementarities and macroeconomics*. Cambridge University Press, p. 163.

Couzin, Iain D., Jens Krause, Nigel R. Franks and Simon A. Levin (2005). "Effective leadership and decision-making in animal groups on the move". In: *Nature* 433.7025, pp. 513–516.

Crow, James F. and Motoo Kimura (1970). *An introduction to population genetics theory*. New York: Harper & Row.

Currie, Thomas E and Ruth Mace (2011). "Mode and tempo in the evolution of socio-political organization: reconciling 'Darwinian' and 'Spencerian' evolutionary approaches in anthropology". In: *Philosophical transactions of the Royal Society B: Biological Sciences* 366.1567, pp. 1108–17.

Dahrendorf, Ralf (1959). *Class and class conflict in industrial society*. Stanford: Stanford University Press.

Dal Bó, Ernesto, Pedro Dal Bó and Jason Snyder (2009). "Political dynasties". In: *Review of Economic Studies* 76, pp. 115–142.

Darwin, Charles (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray.

Dawson, James (1881). *Australian Aborigines*. Cambridge: Cambridge University Press.

Dean, Lewis G., Gill L. Vale, Kevin N. Laland, Emma Flynn and Rachel L. Kendal (2014). "Human cumulative culture: A comparative perspective". In: *Biological Reviews* 89.2, pp. 284–301.

Deffuant, Guillaume, David Neau, Frederic Amblard and Gerard Weisbuch (2000). *Mixing beliefs among interacting agents*. Tech. rep.

Diamond, Jared M. (1997). *Guns, germs, and steel : the fates of human societies*. W.W. Norton & Co.

Diehl, Michael William. (2000). *Hierarchies in action : Cui bono?* Center for Archaeological Investigations, Southern Illinois University, Carbondale, p. 380.

Dikotter, Frank. (2011). *Mao's Great Famine: The history of China's most devastating catastrophe, 1958-62*. Bloomsbury, p. 420.

Dong, Yali, Tatsuya Sasaki and Boyu Zhang (2019). "The competitive advantage of institutional reward". In: *Philosophical transactions of the Royal Society B: Biological Sciences* 286.1899, p. 20190001.

Duda, Pavel and Jan Zrzavý (2013). "Evolution of life history and behavior in Hominidae: Towards phylogenetic reconstruction of the chimpanzee-human last common ancestor". In: *Journal of Human Evolution* 65.4, pp. 424–446.

Dunbar, R.I.M. (1992). "Neocortex size as a constraint on group size in primates". In: *Journal of Human Evolution* 22.6, pp. 469–493.

Dye, David H. (2009). *War paths, peace paths : an archaeology of cooperation and conflict in native eastern North America*. AltaMira Press, p. 217.

Dyson-Hudson, Rada and Eric Alden Smith (1978). "Human teritoriality: an ecological reassessment". In: *American Anthropologist* 80.1, pp. 21–41.

Earle, Timothy (1987). "Chiefdoms in archaeological and ethnohistorical perspective". In: *Annual Review of Anthropology* 16.1, pp. 279–308.

Earle, Timothy (1989). "The evolution of chiefdoms". In: *Current Anthropology* 30.1, pp. 84–88.

Edelstein, J. David (1967). "An organizational theory of union democracy". In: *American Sociological Review* 32.1, p. 19.

Eisenstadt, S. N. and Louis Roniger (1980). "Patron-client relations as a model of structuring social exchange". In: *Comparative Studies in Society and History* 22.1, pp. 42–77.

Engel, Christoph (2010). "Dictator games: A meta study". In: *Preprints of the Max Planck Institute for Research on Collective Goods, No. 2010,07.*

Erdős, P and A Renyi (1959). "On random graphs I". In: *Publicationes Mathematicae* 6, pp. 290–297.

Fiedler, Fred.E. (1964). "A contingency model of leadership effectiveness". In: *Advances in Experimental Social Psychology* 1, pp. 149–190.

Flannery, Kent V. and Joyce. Marcus (2012). *The creation of inequality : How our prehistoric ancestors set the stage for monarchy, slavery, and empire*. Harvard University Press, p. 631.

Foster, K. R. (2004). "Diminishing returns in social evolution: The not-so-tragic commons". In: *Journal of Evolutionary Biology* 17.5, pp. 1058–1072.

Fowler, James H. (2005). "Human cooperation: Second-order free-riding problem solved?" In: *Nature* 437.7058, E8–E8.

Frank, Steven A. (1998). *Foundations of social evolution*. Princeton University Press, p. 268.

Friesen, T. Max (1999). "Resource structure, scalar stress, and the development of Inuit social organization". In: *World Archaeology* 31.1, pp. 21–37.

Galam, Serge and Frans Jacobs (2007). "The role of inflexible minorities in the breaking of democratic opinion dynamics". In: *Physica A: Statistical Mechanics and its Applications* 381, pp. 366–376.

Gardner, A., S. A. West and G. Wild (2011). "The genetical theory of kin selection". In: *Journal of Evolutionary Biology* 24.5, pp. 1020–1043.

Garfield, Zachary H., Robert L. Hubbard and Edward H. Hagen (2019a). "Evolutionary models of leadership". In: *Human Nature*, pp. 1–36.

Garfield, Zachary H., Christopher von Rueden and Edward H. Hagen (2019b). "The evolutionary anthropology of political leadership". In: *Leadership Quarterly* 30.1, pp. 59–80.

Garland, Joshua, Andrew M. Berdahl, Jie Sun and Erik M. Bollt (2018). "Anatomy of leadership in collective behaviour". In: *Chaos* 28.7.

Gat, Azar (2015). *Proving communal warfare among hunter-gatherers: The quasi-rousseauan error.*

Gavrilets, Sergey, Jeremy Auerbach and Mark Van Vugt (2016). "Convergence to consensus in heterogeneous groups and the emergence of informal leadership". In: *Scientific Reports* 6.

Gavrilets, Sergey and Laura Fortunato (2014). "A solution to the collective action problem in between-group conflict with within-group inequality". In: *Nature communications* 5.

"Gilets jaunes: The French uprising" (2019). In: *Le monde diplomatique*.

Gintis, Herbert, Carel Van Schaik and Christopher Boehm (2015). "Zoon Politikon: The evolutionary origins of human political systems". In: *Current Anthropology* 56.3, pp. 327–353.

Giraldeau, Luc-Alain and Barbara Livoreil (1998). "Game theory and Social foraging". In: *Game theory and animal behavior*. Ed. by Lee Alan Dugatkin and Hudson Kern Reeve. Chap. 2.

Glowacki, Luke and Chris von Rueden (2015). "Leadership solves collective action problems in small-scale societies". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 370.1683.

Guala, Francesco (2012). "Reciprocity: Weak or strong? What punishment experiments do (and do not) demonstrate". In: *Behavioral and Brain Sciences* 35.01, pp. 1–15.

Hatch, J.W. (1987). "Mortuary indicators of organizational variability among the Southwestern U.S. chiefdoms". In: *Chiefdoms in the Americas*. Rowman & Littlefield.

Hayden, Brian (2001). "Richman, poorman, beggarman, chief: the dynamics of social inequality". In: *Archaeology at the Millennium*. Boston, MA: Springer US, pp. 231–272.

Hayden, Brian and Suzanne Villeneuve (2010). "Who benefits from complexity? A view from Futuna". In: *Pathways to Power*. Springer New York. Chap. 5, pp. 95–145.

Hewlett, B. S., H. N. Fouts, A. H. Boyette and B. L. Hewlett (2011). "Social learning among Congo Basin hunter-gatherers". In: *Philosophical transactions of the Royal Society B: Biological Sciences* 366.1567, pp. 1168–1178.

Hill, Kim, Michael Barton and A. Magdalena Hurtado (2009). "The emergence of human uniqueness: Characters underlying behavioral modernity". In: *Evolutionary Anthropology* 18.5, pp. 187–200.

Holley, Richard A. and Thomas M. Liggett (1975). "Ergodic theorems for weakly interacting infinite systems and the voter model". In: *The Annals of Probability* 3.4, pp. 643–663.

Hook, Ernest and Sidney Hook (1933). *Towards the understanding of Karl Marx: A revolutionary interpretation.* New York: John Day Co.

Hooper, Paul L., Hillard S. Kaplan and James L. Boone (2010). "A theory of leadership in human cooperative groups". In: *Journal of Theoretical Biology* 265.4, pp. 633–646.

Hooper, Paul L., Eric A. Smith, Timothy A. Kohler, Henry Wright and Hillard S. Kaplan (2015). "Ecological and social dynamics of territoriality and hierarchy formation". In: *Principles of Complexity: An Introduction to Complex Adaptive Systems and Human Societies*, pp. 1–12.

Hurwicz, Leonid (1996). "Institutions as families of game forms". In: *The Japanese Economic Review* 47.2, pp. 113–132.

Jalili, Mahdi (2013). "Social power and opinion formation in complex networks". In: *Physica A: Statistical Mechanics and its Applications* 392.4, pp. 959–966.

Johnson, Gregory A (1982). "Organizational structure and scalar stress". In: *Theory and Explanation in Archaeology.* New York: Academic Press, pp. 389–421.

Johnstone, Rufus A. (2000). "Models of reproductive skew: A review and synthesis". In: *Ethology* 106.1, pp. 5–26.

Johnstone, Rufus A and Michael A Cant (1999). "Reproductive skew and the threat of eviction: a new perspective". In: *of the Royal Society B: Biological Sciences* 266, pp. 275–279.

Johnstone, Rufus A. and Andrea Manica (2011). "Evolution of personality differences in leadership". In: *Proceedings of the National Academy of Sciences* 108.20, pp. 8373–8378.

Jones, Eric E. and Janice R. Kelly (2007). "Contributions to a group discussion and perceptions of leadership: Does quantity always count more than quality?" In: *Group Dynamics: Theory, Research, and Practice* 11.1, pp. 15–30.

Jones, Martin K. and Xinyi Liu (2009). "Origins of agriculture in East Asia". In: *Science* 324.5928, pp. 730–731.

Judge, Timothy A., Joyce E. Bono, Remus Ilies and Megan W. Gerhardt (2002). "Personality and leadership: A qualitative and quantitative review". In: *Journal of Applied Psychology* 87.4, pp. 765–780.

Junker, Laura (2018). “Chiefdoms, Archaeology of”. In: *International Encyclopedia of the Social & Behavioral Sciences* 3.2.

Kaplan, H. S., P. L. Hooper and M. Gurven (2009). “The evolutionary and ecological roots of human social organization”. In: *Philosophical transactions of the Royal Society B: Biological Sciences* 364.1533, pp. 3289–3299.

Keller, L (1994). “Partitioning of reproduction in animal societies”. In: *Trends in Ecology & Evolution* 9.3, pp. 98–102.

Kelly, Robert L. (2010). “The lifeways of hunter-gatherers: The foraging spectrum”. In: *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*, pp. 1–362.

Kennett, Douglas J, Bruce Winterhalder, Jacob Bartruff and John Erlandson (2009). “An ecological model for the emergence of institutionalized social hierarchies on California’s nothern channel islands”. In: *Pattern and Process in Cultural Evolution*. UC Davis.

King, Andrew J., Dominic D P Johnson and Mark Van Vugt (2009). “The origins and evolution of leadership”. In: *Current Biology* 19.19, R911–R916.

Kohler, Timothy A., Denton Cockburn, Paul L. Hooper, R. Kyle Bocinsky and Ziad Kobti (2012). “The coevolution of group size and leadership: An agent-based public goods model for prehispanic Pueblo societies”. In: *Advances in Complex Systems* 15.01n02, p. 1150007.

Kokko, Hanna (2003). “Are reproductive skew models evolutionarily stable?” In: *Proceedings of the Royal Society B: Biological Sciences* 270, pp. 265–270.

Kracke, Waud H. (1978). *Force and persuasion: Leadership in an Amazonian society*. University of Chicago Press, p. 322.

Krige, Eileen Jensen (1950). *The social system of the Zulus*. Shuter & Shooter, p. 420.

Laland, Kevin N. and Michael J. O’Brien (2011). “Cultural niche construction: An introduction”. In: *Biological Theory* 6.3, pp. 191–202.

Leach, Darcy K (2005). “The iron law of what again ? Conceptualizing oligarchy across organizational forms”. In: *American Sociological Association* 23.3, pp. 312–337.

Leach, Darcy K. (2015). “Oligarchy, Iron Law of”. In: *International Encyclopedia of the Social & Behavioral Sciences: Second Edition* December 2015, pp. 201–206.

Lee, Richard B and Richard Daly (1999). *Cambridge Encyclopedia of Hunters and Gatherers*, pp. 1–22.

Lewis, David K. (David Kellogg) (1969). *Convention : a philosophical study*. Blackwell, p. 213.

Lewontin, R C (1970). “The units of selection”. In: *Annual Review of Ecology and Systematics* 1.

Lieberman, Erez, Christoph Hauert and Martin A. Nowak (2005). “Evolutionary dynamics on graphs”. In: *Nature* 433.7023, pp. 312–316.

Lucas, Henry C. (2012). *The search for survival: Lessons from disruptive technologies*. Praeger, p. 243.

Marmot, Michael (2005). “Social determinants of health inequalities”. In: *Lancet* 365.9464, pp. 1099–1104.

Marshall, Lorna (1960). “!Kung Bushman Bands”. In: *Africa* 30.4, pp. 325–355.

Masuda, Naoki, N Gibert and S Redner (2010). “Heterogeneous voter models”. In: *Physical Review* 82.

Mattison, Siobhan M., Eric A. Smith, Mary K. Shenk and Ethan E. Cochrane (2016). “The evolution of inequality”. In: *Evolutionary anthropology* 25.4, pp. 184–199.

Mayr, Ernst (1993). “Proximate and ultimate causations”. In: *Biology & Philosophy* 8.1, pp. 93–94.

Mesoudi, Alex (2011). *Cultural evolution: How darwinian theory can explain human culture and synthesize the social sciences.* University of Chicago Press.

Michels, Robert (1911). *Political parties: A sociological study of the oligarchical tendencies of modern democracy.* New York: The Free Press.

Miller, Delbert C (1958). “Decision-making cliques in community power structures: A comparative study of an American and English city”. In: *Source: American Journal of Sociology* 64.3, pp. 299–310.

Miller, Melissa B. and Bonnie L. Bassler (2001). “Quorum sensing in bacteria”. In: *Annual Review of Microbiology* 55.1, pp. 165–199.

Mobilia, M, A Petersen and S Redner (2007). “On the role of zealotry in the voter model”. In: *Journal of Statistical Mechanics: Theory and Experiment* 2007.08, P08029–P08029.

Mobilia, Mauro (2003). “Does a single zealot affect an infinite group of voters?” In: *Physical Review Letters* 91.2, p. 028701.

Moran, P. A. P. (1958). “Random processes in genetics”. In: *Proceedings of the Cambridge Philosophical Society* 54, p. 1958.

Mullen, Brian, Eduardo Salas and James E. Driskell (1989). “Salience, motivation, and artifact as contributions to the relation between participation rate and leadership”. In: *Journal of Experimental Social Psychology* 25.6, pp. 545–559.

Nonacs, Peter and Reinmar Hager (2011). “The past, present and future of reproductive skew theory and experiments”. In: *Biological Reviews* 86.2, pp. 271–298.

Okasha, Samir. (2008). *Evolution and the levels of selection.* Clarendon Press, p. 263.

Oosterbeek, Hessel, Randolph Sloof and Gijs van de Kuilen (2004). “Cultural differences in ultimatum game experiments: Evidence from a meta-analysis”. In: *Experimental Economics* 7.2, pp. 171–188.

Ostrom, Elinor (1990). *Governing the commons.* Cambridge University Press.

Otto, Sarah P and Troy Day (2007). *A biologist’s guide to mathematical modeling in ecology and evolution.* Vol. 6. Princeton, NJ: Princeton University Press.

Pérez-Llanos, Mayte, Juan P. Pinasco, Nicolas Saintier and Analia Silva (2018). “Opinion formation models with heterogeneous persuasion and zealotry”. In: *SIAM Journal on Mathematical Analysis* 50.5, pp. 4812–4837.

Pielstick, C. Dean (2000). “Formal vs. informal leading: A comparative analysis”. In: *Journal of Leadership Studies* 7.3, pp. 99–114.

Pindyck, Robert S. and Daniel L. Rubinfeld (2001). *Microeconomics*. Upper Saddle River, N.J.: Pearson/Prentice Hall, p. 700.

Pinhasi, Ron, Joaquim Fort and Albert J. Ammerman (2005). “Tracing the origin and spread of agriculture in Europe”. In: *PLoS Biology* 3.12, pp. 1–9.

Pitt, Jeremy (2017). “Interactional justice and self-governance of open self-organising systems”. In: *2017 IEEE 11th International Conference on Self-Adaptive and Self-Organizing Systems (SASO)*. Tucson, AZ, USA: IEEE.

Powers, Simon T. and Laurent Lehmann (2014). “An evolutionary model explaining the Neolithic transition from egalitarianism to leadership and despotism”. In: *Proceedings of the Royal Society B: Biological Sciences* 281.1791, pp. 20141349–20141349.

Powers, Simon T. and Laurent Lehmann (2017). “When is bigger better? The effects of group size on the evolution of helping behaviours”. In: *Biological Reviews* 92.2, pp. 902–920.

Powers, Simon T., Carel P. Van Schaik and Laurent Lehmann (2016). “How institutions shaped the last major evolutionary transition to large-scale human societies”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1687.

Price, Douglas T. (1995). “Social inequality at the origins of agriculture”. In: *Foundations of social inequality*. Ed. by TD Price and GM Feinman. New York: NY: Plenum Press. Chap. 5, pp. 129–151.

Price, Michael E. and Mark Van Vugt (2014). “The evolution of leader-follower reciprocity: The theory of service-for-prestige”. In: *Frontiers in Human Neuroscience* 8.JUNE, p. 363.

Prins, H.H.T. (1996). *Ecology and behaviour of the African Buffalo: Social inequality and decision-making*. Vol. 65. 3, p. 399.

Pugliese, Francesco, Alberto Acerbi and Davide Marocco (2015). “Emergence of leadership in a group of autonomous robots”. In: *PLoS ONE* 10.9, pp. 1–21.

Rands, Sean A., Guy Cowlishaw, Richard A. Pettifor, Marcus J. Rowcliffe, Rufus A. Johnstone, J. Marcus Rowcliffe and Rufus A. Johnstone (2003). “Spontaneous emergence of leaders and followers in foraging pairs”. In: *Nature* 423.6938, pp. 432–4.

Reeve, H. Kern, Stephen T. Emlen and Laurent Keller (1998). “Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders?” In: *Behavioral Ecology* 9.3, pp. 267–278.

Reeve, H.K. and F.L.W Ratnieks (1993). “Queen-queen conflicts in polygynous societies: Mutual tolerance and reproductive skew”. In: *Queen number and sociality in insects*. Oxfored: Oxford University Press, pp. 45–85.

Roscoe, Paul (2006). “Fish, game, and the foundations of complexity in forager society: The evidence from New Guinea”. In: *Cross-Cultural Research* 40.1, pp. 29–46.

Rosenberg, Alex (2017). “Why social science is biological science”. In: *Journal for General Philosophy of Science* 48.3, pp. 341–369.

Rosenberg, Alexander (2015). *Philosophy of social sciences*. Avalon Publishing.

Rothschild, Joyce and J. Allen Whitt (1986). *The cooperative workplace : Potentials and dilemmas of organizational democracy and participation*. Cambridge University Press, p. 221.

Ruyle, Eugene E (1973). “Slavery, surplus, and stratification on the Northwest Coast: The ethnoenergetics of an incipient stratification system”. In: *Current Anthropology* 14.5, pp. 603–63.

Sapolsky, Robert M. (2005). “The influence of social hierarchy on primate health”. In: *Science* 308.5722, pp. 648–652.

Schelling, Thomas C. (1960). *The strategy of conflict*. Harvard University Press, p. 309.

Schermerhorn, John R. (2012). *Organizational behavior*. Wiley.

Schumpeter, Joseph A. (1942). *Capitalism, socialism & democracy*. Harper and Brothers.

Service, Elman R (1962). *Primitive social organization an evolutionary perspective*. New York: Random House.

Service, Elman R. (Elman Rogers) (1975). *Origins of the state and civilization : the process of cultural evolution*. Norton, p. 361.

Sherif, Muzafer, O J Harvey, B Jack White, William R Hood, Carolyn W Sherif and Christopher D Green (1954). *Intergroup conflict and cooperation: The Robbers cave experiment*. Tech. rep. Houghton Mifflin Company.

Skyrms, Brian (2003). *The stag hunt and the evolution of social structure*. Cambridge University Press, pp. 1–149.

Smith, Bruce D. (2001). “Low-level food production”. In: *Journal of Archaeological Research* 9.1, pp. 1–43.

Smith, Eric Alden and Jung-Kyoo Choi (2007). “The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations”. In: *The model-based archaeology of socionatural systems*. Santa Fe: SAR Press, pp. 105–119.

Smith, Eric Alden, Monique Borgerhoff Mulder, Samuel Bowles, Michael Gurven, Tom Hertz and Mary K Shenk (2010). “Production systems, inheritance, and inequality in premodern societies”. In: *Current Anthropology* 51.1.

Smith, Jennifer E. et al. (2016). “Leadership in mammalian societies: Emergence, distribution, power, and payoff”. In: *Trends in Ecology and Evolution* 31.1, pp. 54–66.

Sood, V., Tibor Antal and S. Redner (2008). “Voter models on heterogeneous networks”. In: *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* 77.4, p. 041121.

Spencer, Charles S. (1990). “On the tempo and mode of state formation: Neoevolutionism reconsidered”. In: *Journal of Anthropological Archaeology* 9.1, pp. 1–30.

Spisak, Brian R, Michael J O ’brien, Nigel Nicholsong and Mark Van vugt (2015). “Niche construction and the evolution of leadership”. In: *Academy of Management Review* 40.2, pp. 291–306.

Summers, Kyle (2005). “The evolutionary ecology of despotism”. In: *Evolution and Human Behavior* 26.1, pp. 106–135.

Sussman, R (1999). *Primate Ecology and Social Structure (Vol. 1)*. Vol. 1, pp. 3–37.

Szathmáry, E (2015). “Toward major evolutionary transitions theory 2.0”. In: *Proceedings of the National Academy of Sciences* 112.33, pp. 10104–10111.

Szathmáry, E and J M Smith (1995). “The major evolutionary transitions”. In: *Nature* 374.6519, pp. 227–232.

Taylor, P. D. (1992). “Inclusive fitness in a homogeneous environment”. In: *Proceedings of the Royal Society B: Biological Sciences* 249.1326, pp. 299–302.

Testart, Alain (1987). “Game Sharing Systems and Kinship Systems Among Hunter-Gatherers”. In: *Man* 22.2, p. 287.

Tinbergen, N. (1963). “On aims and methods of Ethology”. In: *Zeitschrift für Tierpsychologie* 20.4, pp. 410–433.

Tolbert, Pamela S (2010). “Robert Michels and the Iron Law of Oligarchy”. In: *Blackwell Encyclopedia of Social and Political Movements*. Oxford: Wiley-Blackwell.

Turchin, Peter et al. (2015). “Seshat: The global history databank”. In: *Cliodynamics: The Journal of Quantitative History and Cultural Evolution* 6.1.

Turnbull, Colin M. (1962). *The forest people*. Simon & Schuster, p. 295.

Van Vugt, Mark, Anjana. Ahuja and Mark Van Vugt (2011). *Naturally selected : The evolutionary science of leadership*. HarperBusiness, p. 262.

Van Vugt, Mark, Roy Baumeister, Robin Dunbar, Bob Hogan, Rick O ’gorman, Pete Richerson, Constantine Sedikides and David Sloan Wilson (2007). “Evolutionary origins of leadership and followership”. In: *Personality and Social Psychology Review* 10.4, pp. 354–371.

Van Vugt, Mark, Robert Hogan and Robert B. Kaiser (2008). “Leadership, followership, and evolution: Some lessons from the past”. In: *American Psychologist* 63.3, pp. 182–196.

Vandepitte, Florent (2019). *Le petit livre des gilets jaunes*. Ed. by First.

Vehrencamp, Sandra L. (1983). “A model for the evolution of despotic versus egalitarian societies”. In: *Animal Behaviour* 31.3, pp. 667–682.

Von Rueden, Christopher, Michael Gurven, Hillard Kaplan and Jonathan Stieglitz (2014). “Leadership in an egalitarian society”. In: *Human Nature* 25.4, pp. 538–566.

Von Rueden, Christopher and Mark Van Vugt (2015). “Leadership in small-scale societies: Some implications for theory, research, and practice”. In:

Walker, Reena H., Andrew J. King, J. Weldon McNutt and Neil R. Jordan (2017). “Sneeze to leave: African wild dogs (Lycaon pictus) use variable quorum thresholds facilitated by sneezes in collective decisions”. In: *Proceedings of the Royal Society B: Biological Sciences* 284.1862.

Weingast, Barry R (1997). “The political foundations of democracy and the rule of law”. In: *American Political Science Review* 91.2, pp. 245–263.

West, Stuart A., Ashleigh S. Griffin and Andy Gardner (2007). "Evolutionary explanations for cooperation". In: *Current Biology* 17.16, pp. 661–672.

Wittfogel, karl August (1957). *Oriental despotism: A comparative study of total power*. Yale University Press.

Woodburn, James (1982). "Egalitarian Societies". In: *Man* 17.3, pp. 431–451.

Wright, S (1931). "Evolution in mendelian populations". In: *Genetics* 16.2, pp. 97–159.

Wright, S (1938). "Size of population and breeding structure in relation to evolution". In: *Science* 87, pp. 430–431.

Yang, Dennis Tao (2008). "China's agricultural crisis and famine of 1959 - 1961: A survey and comparison to Soviet famines". In: *Comparative Economic Studies* 50.1, pp. 1–29.

Zeitzen, Miriam Koktvedgaard. (2008). *Polygamy: A cross-cultural analysis*. Bloomsbury 3PL, p. 206.