Social evolution revisited

Abstract

Ever since Charles Darwin published his original thesis on evolution, there has been an on-going quest for a theory to also explain cooperation, especially intraspecific cooperation, otherwise known as social evolution. Various attempts have since been made to provide a comprehensive explanation for the emergence of cooperation between conspecifics. Here we show a theoretical progressive evolutionary pathway, starting with generic self-same agents going through a staged process of competition and cooperation, culminating in the formation of new autonomous super-organisms comprised of evolved versions of the original agents. By pairing-back the concept of the organism to its energetic universality, this approach makes use of well-established ideas, such as life history theory and game theory, to construct a layered framework, showing how intraspecific competitive and cooperative interactions can, over successive generations, follow a logical progression towards increasing sophistication. As a species evolves, the way the organisms compete and cooperate can be clearly identified with characterizable outcomes, such as selecting for enlargement or increased off-spring numbers. This approach represents a potential general theory, explaining how competition and cooperation can evolve within species, providing predictions for behaviours and social structures observable in nature. It may have application well beyond the field of biology and ecology.

Key Words/Phrases: **evolution of cooperation; intraspecific cooperation; social evolution; evolutionary game theory; general theory of evolution**

Introduction

The beauty of Darwin's theory of natural selection is that it is both very simple and generically applicable to all known living systems (Coyne 2009). It is based on a founding assumption that organisms are innately competitive with their conspecifics (Colman 2006). But Darwin himself knew that competition is only part of the story of nature (Darwin 1859). Ever since Darwin's original thesis, a key challenge in evolution science has been to identify the reasons for and mechanisms of cooperation within species (Nowak 2011, Kropotkin 2014, Wilson 2012, Ridley 1997).

Across modern-day species, we observe a wide array of different ways that intraspecific cooperation occurs. If, as deduced through Darwin's theory, all current species came from the same origins (Larson 2004), then by deduction there must be pathways along which they have all evolved – some species remaining competitive, becoming very specialised or highly aggressive, while others have turned to intraspecific cooperation, exhibiting a variety of group and societal structures. There have been several attempts over the last 100 years to explain why and how intraspecific cooperation takes place (Hamilton 1964, Trivers 1971, Maynard Smith 1972, Wilson 1975, Dawkins 1976, Nowak and Sigmund 1998, Nowak 2006, Gardner and West 2006, West et al 2007). Each solution can cater for a selection of observed situations in the present. But none of them alone can comprehensively encapsulate either all types of observation or explain why and how species have achieved their current degrees of cooperation (Rubenstein and Abbot 2017, Sigmund 2010, Wilson 2012). By way of example, inclusive fitness, the theoretical model sitting behind kin selection, has been the favoured way of explaining the on-going cooperation observed in many eusocial insect species. But more recent research has shown this theory to have limitations (Nowak et al 2010) and that, whilst inclusive fitness can help explain to a degree the continuation of eusocial colonies, it does not provide any logical rationale for their origin.

The Modern Synthesis is strongly underpinned by our knowledge of genetics and inheritance. But, under the banner of the Extended Evolutionary Synthesis, a debate has relatively recently arisen about the degree to which evolution is propagated by organisms or alleles (Laland et al 2015). It is felt by some that there is now too much emphasis on the genes (whether considered in terms of competitive alleles or degrees of genetic relatedness), losing sight of the very real physical competition and cooperation that we observe in habitats between organisms themselves.

The quest continues for a theory incorporating the success of Darwin into a broader construct to explain why and how groups and societies are observed to have emerged as evolutionary solutions. In the case of cellular evolution, cooperation has progressed so far as to create new whole cooperative systems – multi-cellular organisms. But how?

The approach presented in this paper represents an attempt to draw these previous explanations together into a logically consistent construct, spanning both competition and cooperation. Starting from a set of basic assumptions universal to all organisms, from bacteria to blue whales, a framework is formulated which caters for numerous evolutionary pathways, along which species can evolve. The outcome is entirely consistent with our understanding of modern genetics and the selfish gene theory, yet it returns more focus onto organisms. And the various existing concepts such as group, inclusive fitness and multilevel selection theories can be seen to emerge as solutions along these pathways. The overall picture shows how species can progress through stages of competition and cooperation to eventually lead to new evolved super-organisms. The framework can cater for all scenarios, from cells competing but eventually cooperating so closely as to produce new whole living organisms, to homo sapiens cooperating sufficiently to create autonomous tribes capable of migrating around the world through hostile landscapes and thereafter forming human society.

Materials and Methods: Assumptions

To construct a universally applicable framework, it is first necessary to identify commonalities to all organisms (also referred to in this paper as agents):

- they are all bounded energetic systems both spatially and temporally (Rosen 1991, Capra 1997, Kauffman 2000), taking in high value energy and producing lower value energy;
- they obtain, digest and process energy and nutrients obtained from their external environment (Morowitz 1968, Nicolis and Prigogine 1977, Schneider and Kay 1994); and
- they undergo a developmental process, involving (1) coming into existence and thereafter survival, (2) growth, and (3) health maintenance (Stearns 1992) (this borrows from the life stages considered to be a founding assumption in life history theory).

Combining these three observations, the generic developmental process can be converted into a priority set of discrete energetic needs, which any organism must satisfy to reach a point of being able to propagate:

- **Level 1 Need (immediate) – Inception and Metabolism**. To process a continuous minimum flow of energy to drive internal processes to satisfy the minute-by-minute through to day-to-day survival requirements of component parts and whole organism. For instance, multicellular organisms must constantly take in oxygen to keep alive the cells of which they are composed.
- **Level 2 Need (short-term) – Structure and Growth**. To direct ingested energy and materials towards becoming structured and larger, to allow (1) storage of energy, to withstand circumstances where immediate energy intake is interrupted; and (2) to achieve sufficient structural size to be able to subsequently replicate or reproduce.
- **Level 3 Need (long-term) – Health and Reproduction**. To power internal processes including catalytic cycles, repair mechanisms and immune system to maintain the metabolic processes and structural integrity until (and beyond) such time as the organism has achieved maturity to replicate or reproduce (including the successful rearing of off-spring).
- **Level 4 Need (spatial)** – There is a fourth need, which will be considered further below (this extends beyond normal life history theory).

(Note that this approach to organism needs parallels Maslow's Hierarchy of Human Needs (Maslow 1943) – a theory in the social sciences – from which it might be construed that there is a Level 5 Need.)

An organism is an energetic biological system driven by its survival requirements (Brown et al 2004). It will prioritise its actions, such that when hungry it forages or hunts (Level 1 need). When hunger is (mostly) satisfied, it may seek to defend a territory or find shelter (Level 2 need), or rest, recuperate and sleep (Level 3 need). The organism needs thereby drive actions in the real physical world, potentially involving interactions with others of its own kind. Clearly the time allocated by any individual to, say, its Level 1 need will be informed by abundance and ease of accessibility of food. In practice, though still hungry, an agent may be forced to rest (Level 3) before resuming foraging or hunting (Level 1). It can therefore be construed as a flexible, not strict, hierarchy of energetic needs, which balances out over time. However, over its bounded life, an organism will not grow if it does not continuously satisfactorily meet its Level 1 needs, and it will not eventually replicate or reproduce if it has not grown (Level 2) and been able to maintain its health (Level 3).

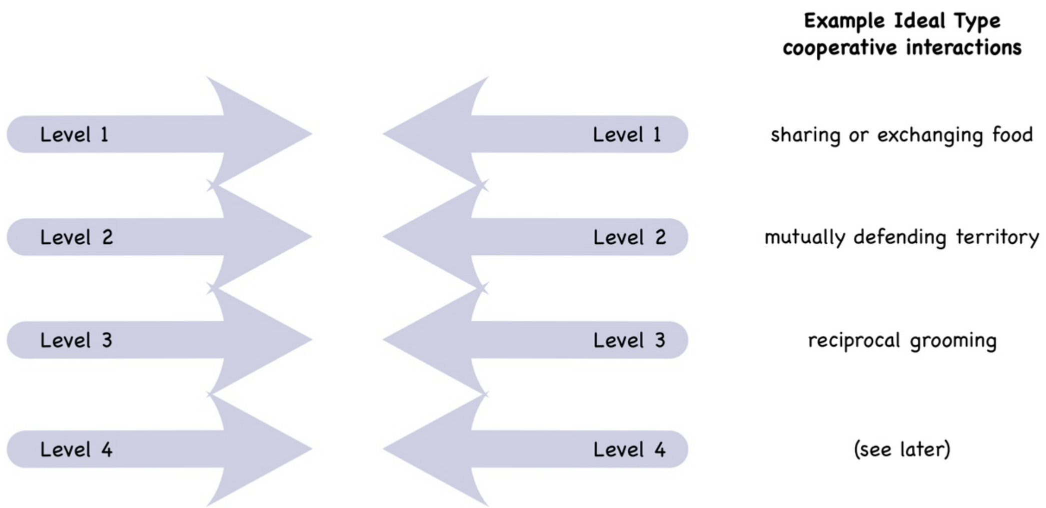
Materials and Methods: Methodology

Introducing Ideal Types of Interaction

A founding assumption for Darwin's theory is that, when food availability is limited, organisms are inherently competitive with their conspecifics – those other agents also needing to access the same sources of food. Taking account of the above identified hierarchy of energetic needs, the basic construct presented here is summarised as follows:

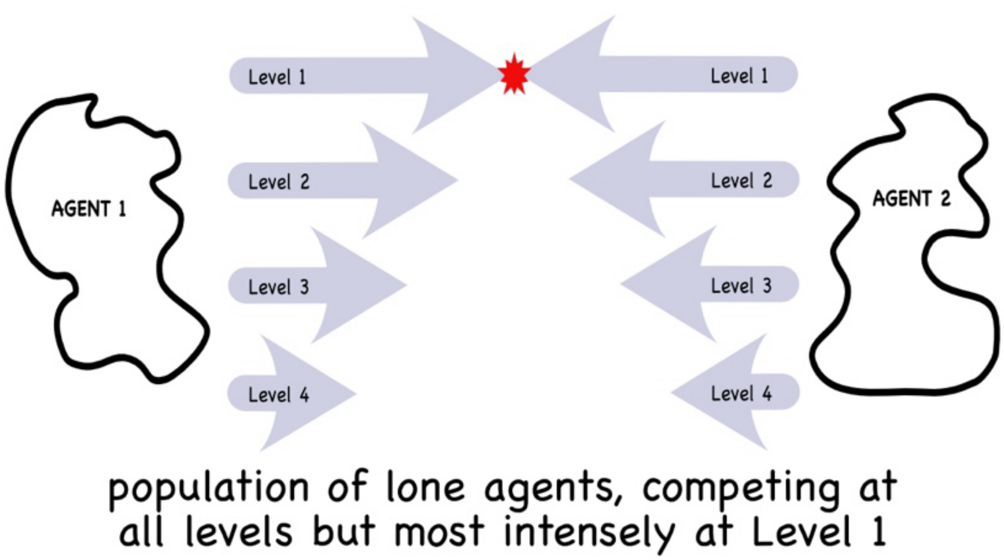
1) each of the identified needs can be interpreted as a specific driver of action and consequently interaction with other conspecifics, giving rise to discrete Ideal Types of competition or cooperation (see Figure 1 for cooperative examples);

Figure 1 – Examples of Ideal Type Interactions



2) the priority order of needs determines the intensity of competition between organisms (say, whilst a population of lone non-cooperating agents compete against other conspecifics in relation to all their needs (Levels 1 to 4), the most intense competition between them is in first instance for their critical Level 1 needs – to find food to eat) (see Figures 2);

Figure 2 – Intensity of competitive interactions for lone competing agents

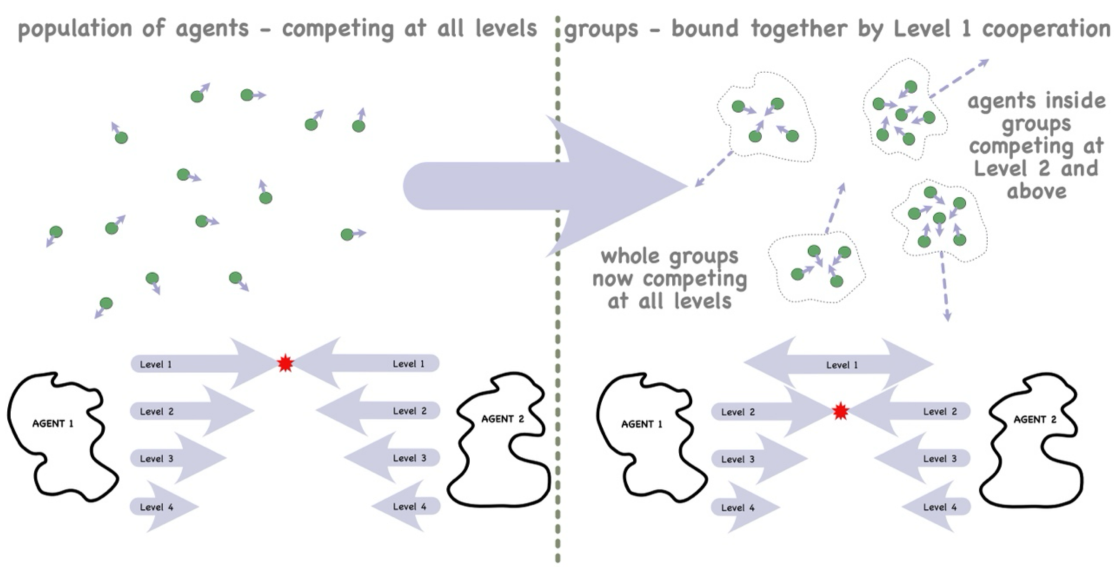


3) cooperation arises out of intense competition (see game theory discussion below), so, when

cooperation does emerge, it begins where competition is most intense, and hence from the bottom (Level 1) upwards;

4) when cooperation emerges, then it gives rise to new or evolved social structuring, within which the erstwhile competition at that level is (mostly) tamed, pushing the most intense competition up to the next level (see Figure 3) - this gives rise to a layered structure of competition and cooperation, so that different evolutionary selection criteria come into play; and

Figure 3 – Transition from Population to Groups

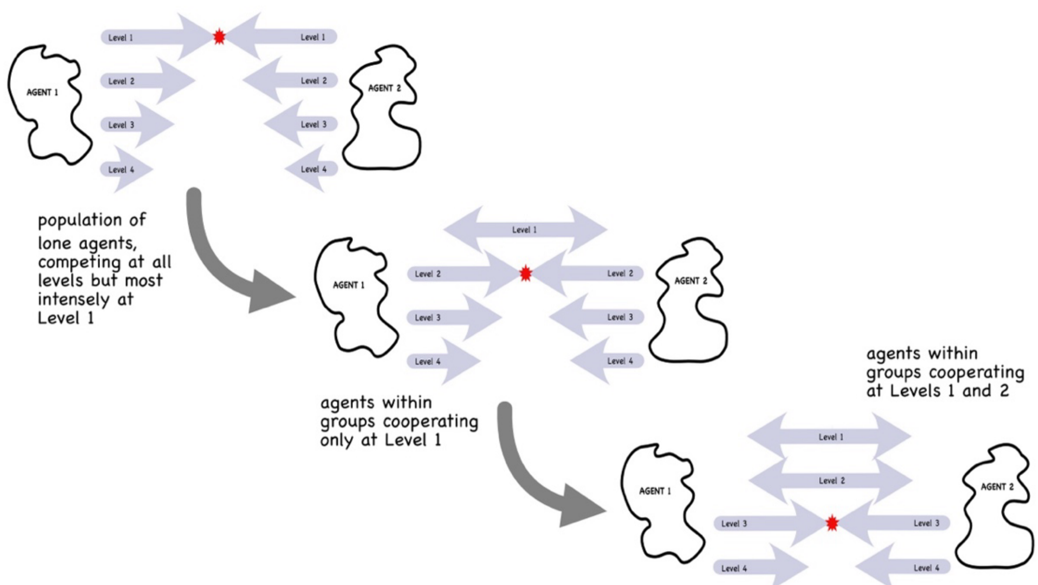


5) though cooperation may arise, binding groups together, individual organisms remain innately competitive entities, causing agents to differentiate in other ways within emergent cooperative social structures.

Putting together this set of statements, starting with a population of lone competing agents, the typical evolutionary progression would see groups of conspecifics first forming through the appearance of Level 1 cooperation (see Figure 3). Inside these groups, though cooperating at

Level 1, the organisms remain competing fiercely with respect to their higher needs (Level 2 and above). Continued progression sees the Level 2 internal (inside the group) competition converting to cooperation, with the most intense internal competition now moving up to Level 3 (see Figure 4). And so on. The nature and degree of the internal competition or cooperation determines how these groups are structured and how the whole groups interact with other groups. The remainder of this paper explores why and how this happens, and the implications.

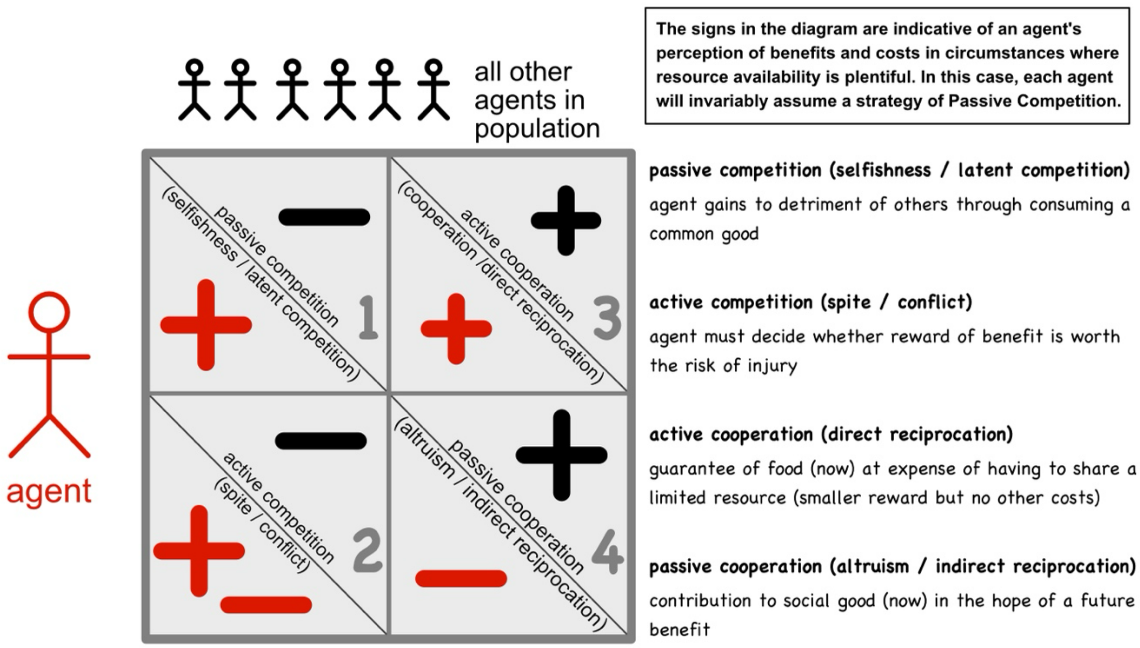
Figure 4 – Progression of Cooperation



Introducing Forms of Interaction

According to evolutionary game theory (Maynard Smith 1982, Nowak 2006), there are four discrete ways two or more agents can interact when competing or cooperating for resources. This is a well-rehearsed construct corresponding to the options set out in the matrix in Figure 5. These are hereafter denoted Forms of Interaction.

Figure 5 – Forms of competition and cooperation



The following descriptions set out how this matrix applies in relation to Level 1 needs (competing or cooperating for food):

1) **Passive Competition** (also denoted selfishness or latent competition) applies where one agent acts independently without any consequences, but their behaviour is in any event detrimental to another party or all other parties in a population. This equates to the selfish party consuming a limited common good (using economic interpretation of the term *common good*), reducing its availability to all others.

2) **Active Competition** (also referred to as spite or conflict) corresponds to circumstances where there is a potential disadvantage from the chosen course of action by each party. Typically, this represents deciding whether to enter into conflict (such as seeking to steal food) with the risk of injury. However, the reward of being able to eat may make the risk worthwhile despite the possible consequence.

3) **Active Cooperation** happens where parties actively choose to cooperate because they can

see a benefit arising. This can be expressed through sharing a limited common good or direct reciprocation. This results in both or all parties obtaining a guaranteed smaller immediate gain (dividing the resource between them) than each could potentially have achieved from a competitive course of action. That reduced gain is now achieved without risk of injury.

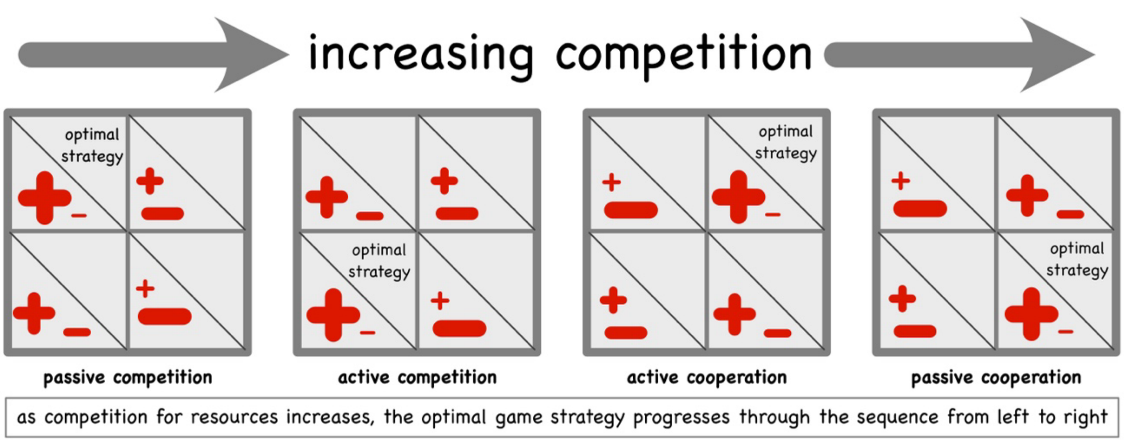
4) **Passive Cooperation** is often referred to as indirect reciprocation or altruism, where one party seemingly contributes to another's benefit without an obvious immediate return. However, in the context of limited resources it can also manifest by avoiding direct competition, such as seeking out a qualitatively different energy source. This can then be accompanied by behavioural changes, including:
   - exchanging different food stuffs, such that each agent benefits from consuming a wider range of nutrients but there is no net flow of energy between them; or
   - contributing to the creation of a *social good* (say, collective store of food) in the expectation that they will each be able to draw from this later.

   This latter cooperative behaviour is only beneficial for any individual if most or preferably all other agents also participate in a cooperative way; otherwise it is a manifestly detrimental strategy for any individual agent.

Looking at this from a purely energetic perspective, competition at any level involves a net flow of energy to one party, where cooperation (active or passive) always ends up fairly with no net flow of energy in either direction (though there might be a time delay before reciprocation occurs). In an idealised scenario of evenly distributed food, there is an equalising effect from competition, such that all organisms in a population experience the same competitive pressures (Tilman 1982). This can be readily modelled in agent-based simulations. At any one time, the benefits and implications of different game strategies will thereby be perceived similarly by all agents in a population.

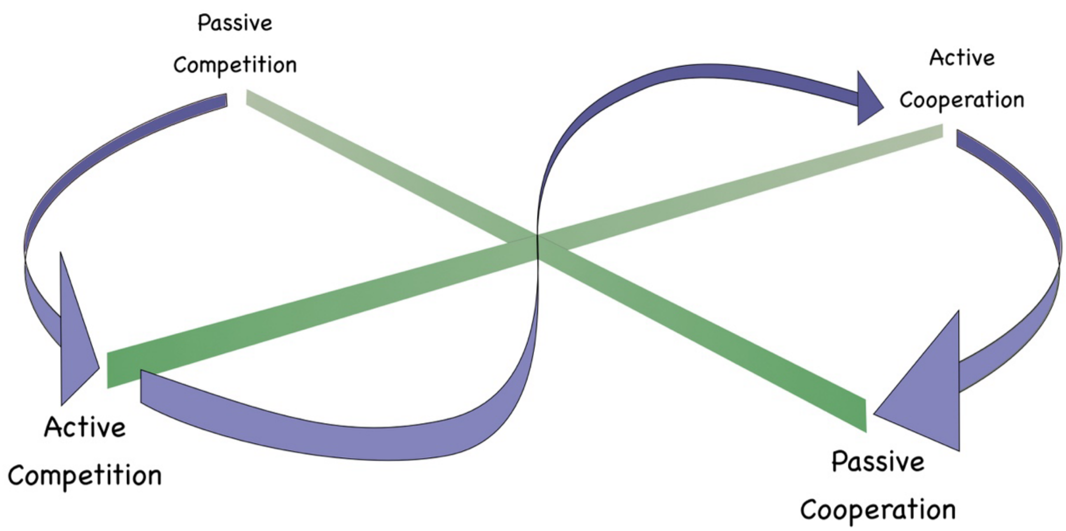
Organisms in first instance seek to avoid conflict (being direct head-to-head competition) (Maynard Smith 1974), because there is a potential cost. So, while food is plentiful, a population of agents will all invariably start by choosing a strategy of Passive Competition. This gives rise to the idealised dispersal solution – agents spreading out evenly across a habitat (Clobert et al 2012), each seeking to be as far apart from all other conspecifics as possible, so that experienced competition for food is minimised. But when population swells or resource is depleted, causing competition to intensify, organisms (or subsequent generations of the same organisms) will be forced to explore alternative game strategies. As competition increases, the benefits and consequences of different strategies alters, as portrayed in Figure 6. Given the equalising effect of competition, the whole population thereby undergoes, what are in effect, a sequence of phase changes, at each step transitioning to new ways of operating.

Figure 6 – Indicative changing perceived benefits and costs of different game strategies



Intensification of competition therefore drives a population of organisms to undergo a logical progression from Passive Competition (i.e. conflict avoidance), through Active Competition, switching to Active Cooperation and finally achieving Passive Cooperation (see Figure 7 - the reason for expressing this on a cruciform will become clear later).

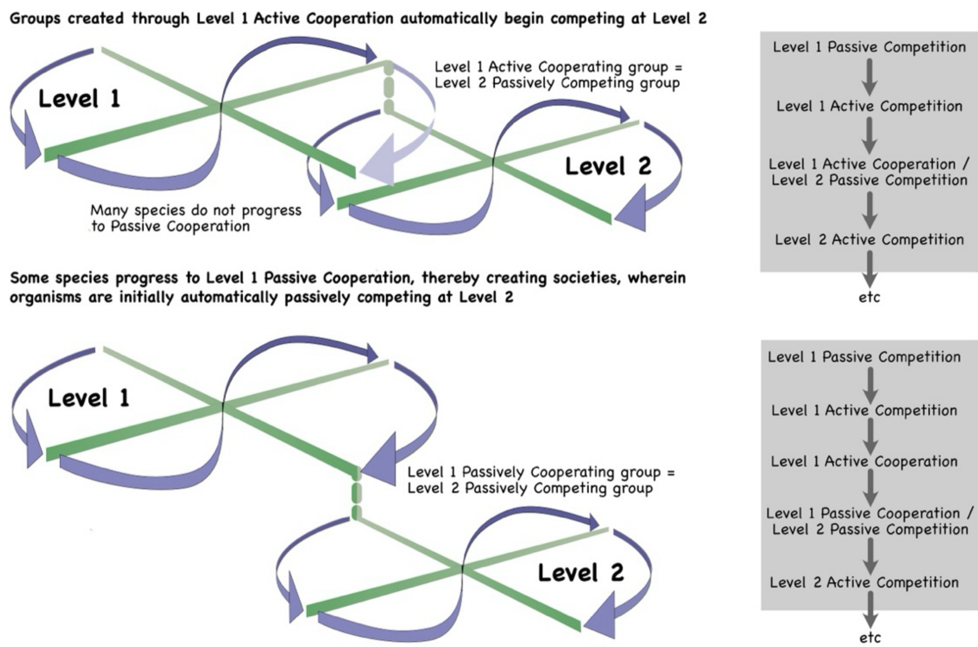
Figure 7 – Sequence of game strategies driven by increasing competition for resources



So far, consideration has primarily been given to Level 1 and acquisition of essential food. However, the same sequence of game strategies (Forms of Interaction) is applicable for all the identified organism needs (Levels 1 to 4). Groups are bound together through Level 1 cooperation, but this does not prevent there from being intense internal competition between agents within such groups in relation to higher needs. A well-known example is that of chimpanzees, where troops are bound together through Level 1 cooperation (sharing fruit), but within those troops the individual chimpanzees compete intensely at all higher levels (Level 2 – growth, and Level 3 – health and reproduction).

There is a relationship between experienced competition without (between groups) and within (between agents inside groups). Hence two neighbouring competing chimpanzee troops, seeking to steal territory off each other, will exacerbate the intensity of competition experienced by all the individuals within each group. When increasing experienced competition reaches inflection points, then following the logic of game theory, Level 2 interactions can also switch to being cooperative and subsequently Levels 3 and 4. This progression is shown in Figure 4 and further portrayed in Figure 8.

Figure 8 – Level 1 sequence of game strategies progressing to Level 2



The outcome is a layered framework, providing the fundamental basis for social evolution. Species can climb this ladder of interaction levels to achieve ever-increasingly sophisticated ways of competing and then cooperating. This gives rise to a hierarchy of system types. When organisms are all competing individually, they represent a population. Where groups exist, with agents internally cooperating at Level 1 but competing at Level 2, then these represent Level 1 systems, etc. Given the hierarchy of needs, agents competing at a lower level (say, Level 1 – for food) cannot cooperate at a higher level (say, Level 3 – mutual grooming) (see Tables 1 and 2).

Table 1 – Hierarchy of system types (bold indicates most intense competition)

System	Population	Level 1	Level 2	Level 3	Level 4
Need 1	**competition**	*cooperation*	*cooperation*	*cooperation*	*cooperation*
Need 2	competition	**competition**	*cooperation*	*cooperation*	*cooperation*
Need 3	competition	competition	**competition**	*cooperation*	*cooperation*
Need 4	competition	competition	competition	**competition**	*cooperation*

Table 2 – Typical Biological Examples of System Types

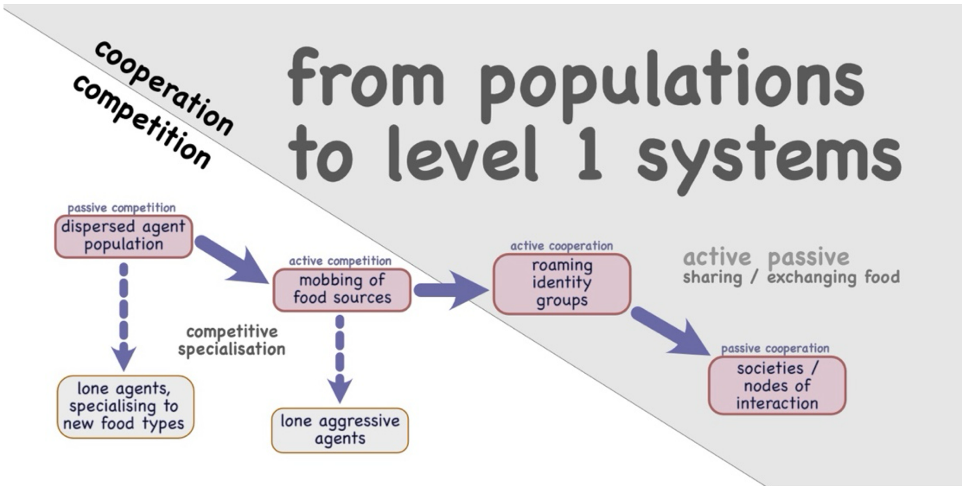
System	**Examples**
System Type 0	Populations of lone agents
System Type 1	Unstructured groups or societies – herds, shoals, flocks
System Type 2	Structured groups (hierarchic / egalitarian) – troops, packs
System Type 3	Layered groups (layering may be overlain onto an existing hierarchy)
System Type 4	Autonomous groups, capable of intentional movement in physical space

Results: The Evolutionary Pathway

The consequence of this set of assumptions and outlined interaction model is now explored to see how this would theoretically play out for an initial hypothetical species of asexual lone autonomous competing agents in an idealised situation of evenly distributed replenishing energy within a bounded area (a habitat). The sequence of evolutionary steps outlined below could take hundreds of millions of years. There arise a series of predictions in terms of evolutionary selection criteria on organisms and emergence of social structures, ultimately leading to the formation of new whole autonomous living systems, from which the whole process can be repeated, giving rise to nested biological structures. (To fit the necessary word count, only very high-level summaries are provided for each stage in the overall pathway.)

Level 1 (see Figure 9)

Figure 9 – From populations to Level 1 Systems Pathway



LEVEL 1 – PASSIVE COMPETITION

Level 1 Passive Competition gives rise to the typical dispersion of a population within a suitable habitat where there is the necessary food for survival. This represents the primary type of competitive evolution that Darwin documented. It provides the arena for selection of the fittest set of traits arising from mutations, allowing successive generations of organisms in a species to become specialised and adapted to different food sources, giving rise to adaptive radiation. The originating species thereby diversifies into a multitude of new forms, new species, each occupying a slightly different energetic niche within a habitat.

LEVEL 1 – ACTIVE COMPETITION

Focussing on one of these newly diversified species, if they prove to be successful and their population swells, then competition for their preferred food will intensify. To avoid conflict, organisms from this species will push outwards into neighbouring habitats. Different selective pressures on those at the fringes will cause them to evolve to form further new species:

speciation. Within the core of the original habitat, foraging alone is now no longer adequate – there are too many others also consuming the same common good. To get enough food to survive, grow, maintain health and replicate, agents need to develop alternative survival strategies. They can learn to watch others to see if they have found any food and then become aggressive, seeking to steal food. These agents prove to be more successful than their timid counterparts. Mutations supporting these attributes will therefore be selected. Consequently, the population transitions into more aggressive agents, mobbing food sources, giving rise to conflict. Good examples of such resource mobbing are provided by the behaviour of sea gulls and various other birds (Ward et al 2002, Cheng et al 2020).

LEVEL 1 – ACTIVE COOPERATION

Within the context of food mobbing, game theory can be applied. Conflict for all agents eventually becomes too frequent and too hazardous and the balance between risk and reward tips, causing the population to flip to cooperation. Cooperation manifests as either sharing discrete quanta of food or direct reciprocation (both equate to the same thing). The huge benefit for individuals that reciprocal sharing confers is to smooth the supply of energy, allowing an organism to eat daily, as opposed to, say, twice a week (see Box 1). Direct reciprocation and sharing require a repeated tit-for-tat cooperation with a limited number of known other agents (Boyd and Richerson 1988). Consequently, as each agent will only benefit from sharing by being actively present, they end up roaming around a habitat (jungle or other) as loosely connected groupings. Certain herd animals, such as bison and elk, may be good examples. For these species, putting aside the breeding season, there is minimal (if any) internal group structure and no evidence of any higher-level cooperation between the agents in these groups.

Box 1 – Transition to cooperation to smooth energy supply

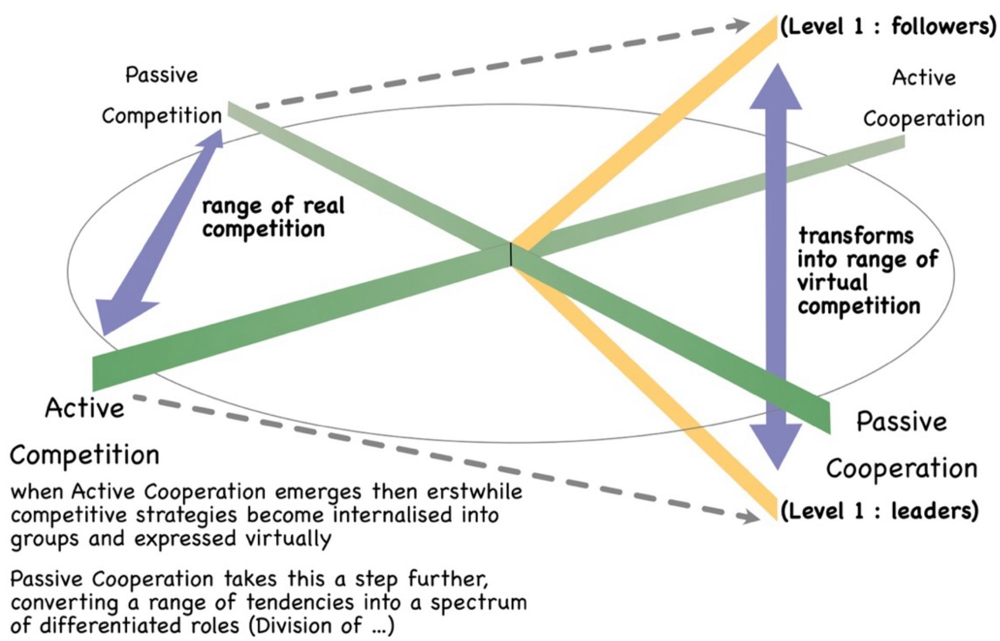
Food usually comes in discrete quanta (clumps of grass, crumbs of bread, fruit in a tree, prey). Whilst many food sources, such as grasses, may appear continuous, in times of drought even these revert to being found in small clumps that must be shared.

Imagine that there is a tree laden with ripening fruit in the jungle. It is quickly mobbed by a population of monkeys, actively competing to get some luscious food. Let's say there are 90 fruits on the tree and 100 monkeys turn up. As active competitors, only 90 of these monkeys can eat because the fruit comes in defined lumps. Those 10 monkeys who don't eat today may not survive until tomorrow. The evolutionary solution to this is that some monkeys, instead of being aggressive and fighting, choose to share fruit. Each of these sharing monkeys now get, say, half a fruit - enough to meet immediate Level 1 needs and survive another day. Given that being aggressive burns energy, being peaceful and sharing has the added benefit of being a more energetically efficient behavioural strategy. It is a finely tuned balance between a guaranteed but reduced amount of food (sharing a fixed resource size), set against potential greater reward with possibility of injury.

The critical outcome of cooperation for individuals is to smooth their food intake. When competition becomes sufficiently continuously intense, then those that choose to cooperate survive better, and pass on their genes, than those who remain actively competing.

For a group to maintain cohesion, it is reliant on the agents within to continuously share food. This requires a behavioural change, selecting for those organisms which are less aggressive in the presence of food. But, as per Darwin's thesis, each agent remains an innately competitive entity. So, previous variation in game strategies between Passive and Active Competition becomes internalised within groups (and expressed virtually). At Level 1 this transforms into a scale from leaders (more innately aggressive) to followers (less aggressive) within the newly formed cooperative groups (see Figure 10) (Aplin et al 2014, Conradt and Roper 2007).

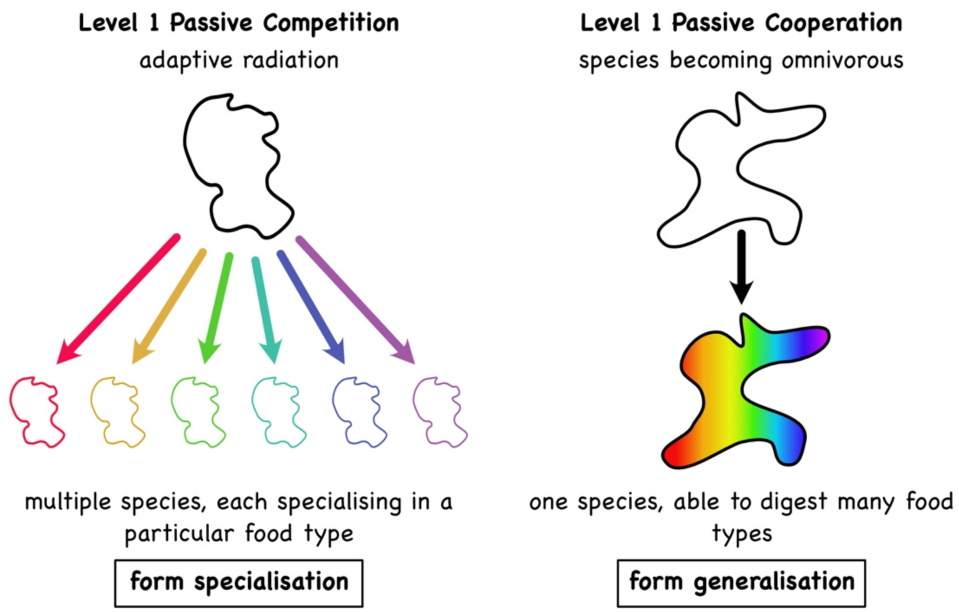
Figure 10 – Internalisation of competition at Level 1



LEVEL 1 – PASSIVE COOPERATION

Now that the species is clumped in groups and sharing food, if food is scarce and agents try out other food types, then instead of diversifying into separate species (as per Level 1 Competition – adaptive radiation and speciation), natural selection favours those adaptations which facilitate organisms becoming opportunistically omnivorous. Heretofore diversification becomes systemically internalised within future generations of the species (see Figure 11). This is hereafter referred to as *form generalisation*, being the opposite to *form specialisation*.

Figure 11 – Emergence of Omnivory



Omnivory provides scope for further behavioural changes, to enable the whole group to benefit from the greater energetic availability provided by a wider variety of food types. Sharing and direct reciprocation interactions can progress to exchanging (say, swapping a blackberry for a raspberry) or indirect reciprocation (contributing to a collective food store). Again, these actions effect the same outcome. However, as explored by others (Nowak 1998), indirect reciprocation can only be a beneficial game strategy if all (or most) other agents play the same game.

Indirect reciprocation involves agents exchanging the same quantity of energy for qualitatively different nutrients. This allows for the emergence of specialist foragers. But, and this is of critical importance, at a collective level these interactions can only be successful for all members of the emergent society through the creation of nodes or focal points of interaction (Kim and Conte 2024). Underlying this is the same principle as caused roaming identity groups to form from Active Cooperation. In the case of Passive Cooperation, static interaction nodes are required for all agents to be able to benefit from exchange and/or indirect reciprocation. (In the human domain, we experience these foci as marketplaces/town centres.) Creation of these focal points represents the originating motivator (or gravitational attractor) for the formation of collective nests, as seen in the social insect world; though most social insects express cooperation that goes well beyond basic Level 1 cooperative systems.

Level 1 Active Cooperation corresponds to repeated direct reciprocal sharing of food between pairs of agents. These paired interactions are the basis of a network, connecting all members of the group, creating a shared identity to bind them together as a unit (a roaming identity group). This ensures that there are no free riders but limits group size (Boyd and Richerson 1988). However, and so long as there are group level mechanisms to preclude free-riders (such as the creation of a common currency), then Passive Cooperation interactions can take place with relative strangers while remaining mutually beneficial. So, Passive Cooperation allows groups to expand to societies, potentially involving millions of agents, as witnessed amongst social insects and in the human domain.

LEVEL 1 – SUMMARY (see Table 3)

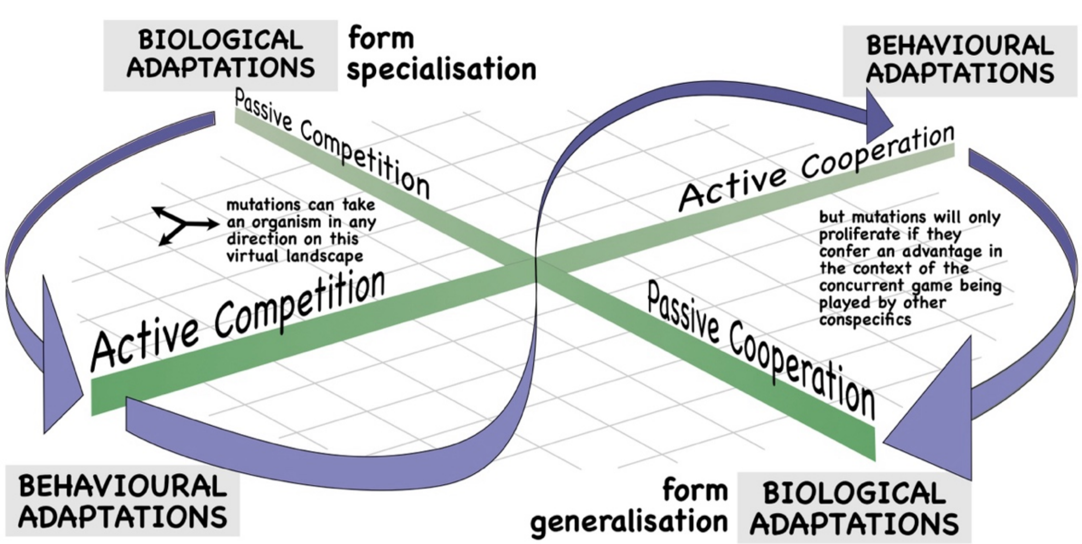
Table 3 – Level 1 – consequences of different game strategies

Level 1	**Individual Response**	**Population / Group Behaviour**
Passive Competition	▪ foraging/hunting/feeding independently ▪ selection for food specialists (biological)	▪ physical dispersal ▪ adaptive radiation
Active Competition	▪ fighting for food ▪ more aggressive (behavioural) ▪ selection for biological adaptations to support behavioural changes (ability to fight for food)	▪ intermittent mobbing of food sources ▪ speciation (those that don't fight for food, driven outwards into new habitats)
Active Cooperation	▪ sharing food (direct reciprocation) ▪ more peaceful in presence of food (behavioural)	▪ roaming as a loose-knit identity groups ▪ emergence of leaders/followers

	▪ selection for peaceful cooperators (herd behaviour)	▪ opportunistic omnivory across groups
Passive Cooperation	▪ opportunistic omnivores ▪ exchanging food or contributing to a social good (indirect reciprocation) ▪ selection for food generalists (biological) (omnivorous)	▪ fixed focal points of interaction for exchange of food types ▪ emergence of societies (large groups) ▪ social good : focal point of interaction and ability to exchange food types with conspecifics (and potentially emergence of currency or equivalent to enable exchange – eg. adenosine triphosphate ATP)

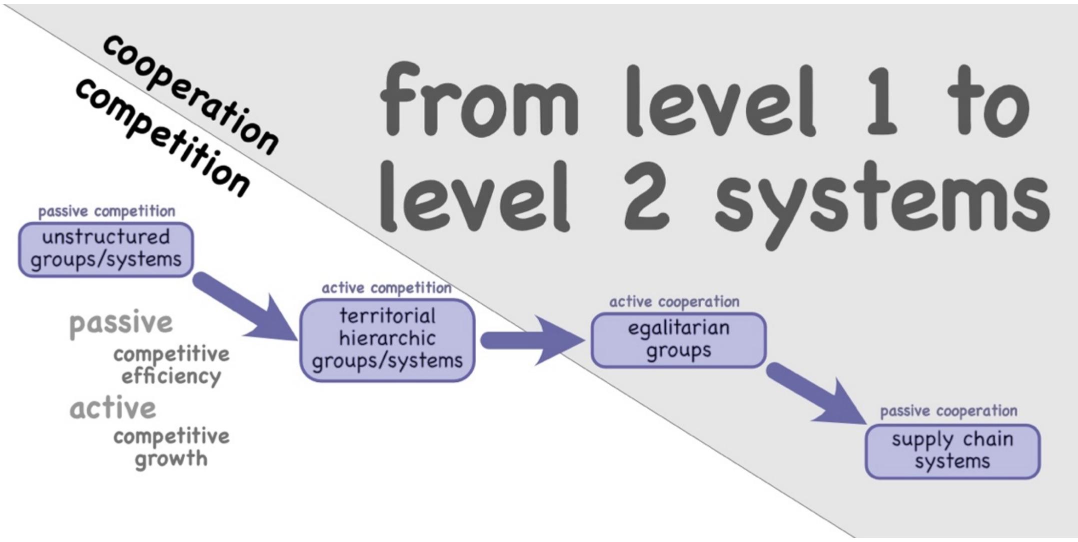
The Forms of Interaction can be plotted out to create an evolutionary landscape as shown in Figure 12. This exists for each Level (1 to 4), creating very specific selection criteria for biological and behavioural mutations as experienced by the competing or cooperating organisms. New mutations will only proffer an advantage to an individual organism if they improve its ability to succeed in the context of the concurrent game strategy being played out by all the other conspecifics. This will tend to push a species towards one or other game strategy until competition becomes so intense that a phase change is required, affecting all organisms at once. This suggests that transitions when they happen might be quite quick. Could this contribute to the observation of punctuated equilibrium? (Eldredge and Gould 1972).

Figure 12 – Evolutionary landscape (applies to each Level)



Level 2 (see Figure 13)

Figure 13 – From Level 1 to Level 2 Systems



A group or society formed through Level 1 cooperation is bound together to become a whole competing unit. The species now operates as a population of competing groups/societies. With supply of energy smoothed through Level 1 sharing and/or exchanging, the most intense competition moves up to Level 2: **competing for rate of intake of food** (Level 2 competition). Inside these groups, the same sequence of strategies (Forms of Interaction) is now pursued. However, with the groups competing at all levels (see Figure 3), there arises a relationship between internal interactions (agents inside groups) and external interactions (between whole groups), as explored further below.

LEVEL 2 – PASSIVE COMPETITION

Conflict avoidance at Level 2 (Passive Competition) is expressed inside the group as needing less food, reducing rate of energy consumption – thereby becoming even more specialist in regard to specific food sources. This is only possible once intake of energy has been smoothed because mutations enabling increased efficiency would not be beneficial and not selected for when food intake is intermittent (simply put, agents can't gain an advantage from being more efficient when all energy obtained is competitively used up in the interval before the next meal). Where a group has become isolated through natural barriers – say, island or valley – then the territory they occupy remains fixed and they are not competing against other whole groups. In these circumstances, Level 2 Passive Competition will dominate. This leads to the well-documented island effect, which gives rise to species evolving to become smaller, to shrink (Foster 1964) – to be more efficient in the use of food on a per agent basis.

LEVEL 2 – ACTIVE COMPETITION

In contrast, Active Competition at Level 2 arises from each agent seeking to maximise the rate of intake of energy. This becomes expressed as competitive growth. This creates evolutionary selective pressure for faster growing organisms progressing to larger adults. This would help explain the long-standing question of what evolutionary pressures drove many dinosaur species to grow so fast and so large. It suggests that those larger dinosaur species must have either functioned in groups or evolved from predecessors which operated in groups.

Whole groups outwardly express the competition experienced within. This intensifies competition between groups, forcing them to become territorial, and to perpetually seek to expand territories. The erstwhile leaders and followers (of Level 1 roaming groups) necessarily adopt a formal hierarchy, typical of chimpanzee troops. This is because the group becomes dependent on the larger and fiercer members to fight for the territory. In compensation for taking a lead in defending their territory, these larger, more aggressive group members get priority access to food (amongst other benefits). This feedback between individual and group behaviour reinforces the competitive growth dynamic – the larger organisms being more reproductively successful, the species becoming ever larger generation-on-generation.

LEVEL 2 – ACTIVE COOPERATION

The transition to agent cooperation inside groups is driven by external group competition. A group, which is reliant on a single largest member to fight for them to defend their territory, will be less successful than a group, which learns to act as a coherent fighting unit, where all individuals stand together as a team to defend their patch of land. This requires a behavioural and cultural adaptation: for members of the group to become more predictable towards each other and trust that their groupmates will hold the line when threatened.

Trust within the group must be built on a day-to-day basis through greater predictability. Previous behaviour, where a leader may erratically threaten and take out their anger on lower ranking members of the group, would no longer be culturally tolerated. And, it becomes necessary for food to be distributed more equitably, so that all members of the group have the potential to grow to a similar size and strength. These cultural adaptations have biological consequences (see Figure 12), such as moving away from the competitive growth dynamic. In these more egalitarian groups, being larger no longer improves chances of survival and reproduction. Hence variation in adult organism size across the species diminishes.

When territory sizes are closely dependent on the strength of the largest organisms, there is a tendency for areas to wax and wane according to the health and age of those lead individuals. As with chimpanzees, neighbouring troops are constantly at war, always seeking out opportunities to expand territory. But when egalitarian groups displace the more hierarchic ones, then territorial areas and boundaries between groups stabilise – Level 2 cooperation within groups allowing for less territorial conflict between them.

When Level 2 cooperation emerges, the erstwhile range of real physical competitive strategies (efficiency versus growth) becomes internalised through individual agents seeking to differentiate themselves within the newly cooperative environment. The prior Level 1 demarcation of leaders and followers becomes nuanced, converting into a division of labour. This is typically expressed through the more aggressive individuals taking on defensive roles and the remainder focussing on foraging. This can be seen amongst a wide array of species from meerkats to various types of monkeys.

LEVEL 2 – PASSIVE COOPERATION

Passive Cooperation at Level 2 becomes expressed by means of a transition to forced omnivory (compared to opportunistic omnivory at Level 1). With competitive growth tamed, Level 2 actively cooperative groups must inhabit a limited fixed territory (no longer waxing and waning). To maximise their access to energy within that bounded space, these egalitarian groups are forced to try out a broader selection of foods. Those able to digest a wider diversity of foods survive better, with evolution progressing to the point of agents becoming fully dependent on eating a variety of food types.

At Level 1, opportunistic omnivory and participation in material or energetic exchange activity was dependent on the creation of interaction nodes. At Level 2, dependent omnivory is contingent on the creation of formal supply chains to and from those same interaction nodes to ensure that all agents in the social system can have regular and sustained access to a variety of food types. Supply chains arise out of the simultaneous carrying out of different tasks. As evidenced from human economic history (Sun 2012), these are reliant on formal divisions of labour (probably better termed *exchange of labour* – to be consistent with *exchange of energy and materials* at Level 1 and the interaction model presented earlier).

This system-level requirement for simultaneous achievement of different tasks creates selective pressure for mutations enabling further *form generalisations* – this time (at Level 2) in relation to activities rather than ingestion of foods. These are most obviously expressed in the insect world, where identical agents at inception grow into different task players as adults, such as soldiers and workers. It is, then, the organism's template (the DNA) which has undergone form generalisation, allowing for specialised adult agents; again, this is the opposite effect to Passive Competition (see Figure 12), which at Level 2 gave rise to an accentuation of speciation (greater efficiency in regard to a particular survival strategy). The outcome of this process is the creation of a society capable of creating a Level 2 social good – in this case a collective safe space and secure store of food for the benefit of all – a nest or hive. The relationship and dependency between whole and parts has become further intertwined.

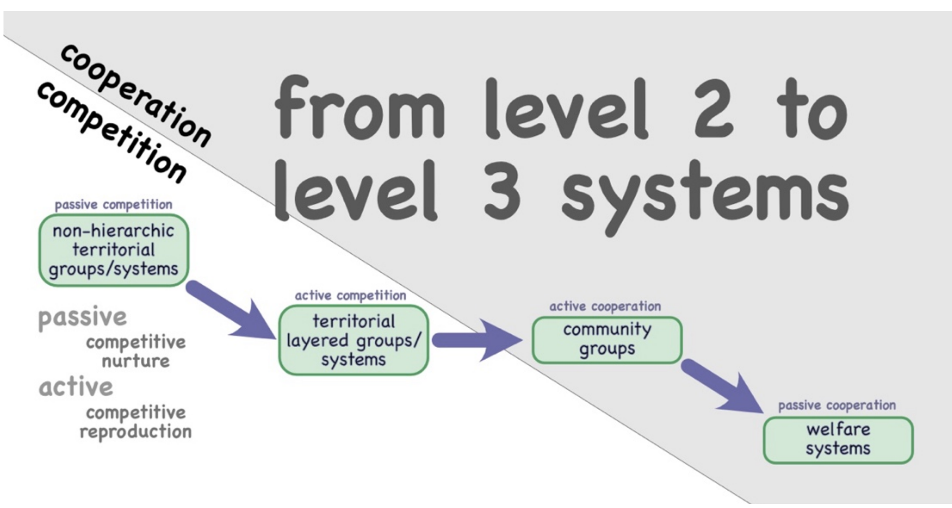
LEVEL 2 – SUMMARY (see Table 4)

Table 4 – Level 2 – consequences of different game strategies

Level 2	**Individual Response**	**Population / Group Behaviour**
Passive Competition	▪ avoiding competition for food within group ▪ selection for improved efficiency at digesting existing food types (energetic efficiency/size reduction) (biological) – activity specialists	▪ roaming unstructured groups/societies (as per Level 1 Active/Passive Cooperation)
Active Competition	▪ fighting for control of territory (i.e. rank in hierarchy) ▪ more capable at defending territory (behavioural) ▪ selection for biological adaptations to support behavioural changes (growth/enlargement and unpredictability)	▪ territorial (ever expanding) hierarchical groups/societies ▪ landscape divided into territories, each occupied by membership group
Active Cooperation	▪ sharing territory (direct reciprocation in defence activity) ▪ selection for more predictable and trustworthy cooperators (behavioural) ▪ no longer competing for size	▪ territorial (fixed size) structured egalitarian (matrix) membership groups ▪ emergence of division (exchange) of labour ▪ dependent omnivory across group
Passive Cooperation	▪ dependent omnivores ▪ exchanging activities (i.e. some specialising in foraging and others in defence) ▪ selection for activity generalists (organisms capable of growing into different adult roles / forms)	▪ structured territorial membership societies ▪ formation of supply chains to focal points of interaction ▪ social good : rules of collective behaviour, stores of food and defendable constructed space

Level 3 (see Figure 14)

Figure 14 – From Level 2 to Level 3 Systems



The underlying dynamic at Level 3 is **competition for total energy consumption**. This is expressed through each organism seeking to divert as much energy as possible towards maintaining its own health and the production of off-spring.

When this whole framework is considered from a system thinking perspective, Level 2 systems represent linear systems, which can grow additively. Level 2 internally competitive systems express such growth in fractal form (plants, hierarchies and bureaucracies), whereas Level 2 internally cooperative systems express growth as matrices (such as crystalline substances). Level 3 systems involve the retention of energy and materials within a system through cyclic processes. Level 3 systems express growth through creating more cycles, whether that is through increased numbers of internal cycles (such as a complexifying immune system) or through replication or reproduction of whole units. Hence, at Level 3, there is an intimate relationship between health maintenance and reproduction. Another consequence of this differentiation between Level 2 and Level 3 systems is that linear growth naturally leads to vertical and hierarchic structures (think – solid structures, such as plants and skeletons), whereas cyclic systems tend to produce layered and cyclic structures (think – fluids, layering, skins and membranes).

LEVEL 3 – PASSIVE COMPETITION

The differential between Level 3 Passive and Active Competition is acknowledged in life history theory with the observation of different reproductive strategies known as k-selection and r-selection (Stearns 1992). Level 3 Passive Competition (k-selection) sees organisms looking after their and their off-springs' health independently, avoiding experienced competition. The success of each next generation is entirely dependent on the continued health of the direct parent(s), regardless of any other internal group cooperation (at Levels 1 and 2). A consequence of this competitive solution is to extend agent lifespans, where ultimate reproductive success of an agent and thence genetic contribution to the future species is measured over number of sequential birthings or broods. In groups where Level 3 Passive Competition dominates, then there will be minimal if any social layering.

LEVEL 3 – ACTIVE COMPETITION

Level 3 Active Competition (r-selection) takes matters in the opposite direction. It is expressed in terms of competing for greater frequency of reproduction or number of offspring – each organism competing to convert as quickly as possible as much energy as it can into the propagation of its genes. This represents competitive reproduction and taken to its logical conclusion can lead to the formation of millions of eggs or young. If there are huge numbers of off-spring, then they will be competing for the same source of energy as the adults. The evolutionary solution to this has been to give rise to differentiation in forms between adults and off-spring, so that they can depend upon different energy sources. This is normally referred to as resource partitioning, such as grubs and mature organisms in the insect world. It is an example of lifespan layering within a species. It is quite different to the DNA form generalisation discussed earlier.

Turning to familiar species, such as apes and monkeys, imagine starting with a typical hierarchic group. A key perk for higher ranking members of such groups is to receive grooming from lower ranking individuals. Grooming is a Level 3 interaction, benefiting those receiving attention and representing expenditure of energy for those giving such assistance. For those at the same level of such hierarchies, grooming will tend to be mutual and equitable (no net flow of energy). This equivalence strengthens these horizontal relationships and has the effect of creating social layers across the group.

Where a hierarchy already exists, then this Level 3 horizontal structure simply maps onto and reinforces the existing vertical hierarchy, ultimately measured in terms of greater reproductive success for those in the top layers. If, however, a social hierarchy has been moderated through Level 2 cooperation, then Level 3 social layering can be more readily observed. A good example is provided by bonobos, where social structure is more layered than the strict vertical hierarchies seen in chimpanzee troops. There is a further evidence that bonobos have evolutionarily progressed beyond chimpanzees: bonobos have never been observed carrying out infanticide where chimpanzees have, suggesting that chimpanzees continue to compete inside their troops at Level 3.

LEVEL 3 – ACTIVE COOPERATION

In groups where there is strong hierarchic layering, then reproductive success is strictly focussed on those in the higher layers. Those in lower layers will have poorer health and less able to rear healthy young. At a group level, this means reproduction is limited and not making optimal use of the entire genetic stock of the group. If, however, mutually reciprocal grooming, as occurs within layers in Level 3 Active Competition groups, expands to encompass all members of a group, then the whole can become more reproductively successful.

When grooming expands to become reciprocal amongst all members of a group, heretofore strong layering will be muted. This creates a community, representing a web of mutualistic paired nurture interactions across the whole group. These Level 3 reciprocal bonds are similar to that holding groups together through Level 1 food sharing interactions, but as they correlate to a Level 3 need (health and nurture), they are invariably weaker.

Given the time required for each individual to give such reciprocation (generally expressed as grooming), each agent can sustain only a small number of reciprocal friends. This limits community size. But through better nurture for all, whole groups can be reproductively more successful; and their numbers swell. Groups (bound together through Level 1 cooperation) therefore grow and internally splinter into different internal communities. Eventually, at sufficient size of group the Level 1 and Level 2 bonds that hold the whole group together are insufficient. Consequently, these internal communities split apart, converting into entirely new groups, needing their own territories. This represents replication of whole groups. When competition is intense, then, on evolutionary timescales, those groups which express Level 3 Active Cooperation will eventually displace those that don't – at Level 3 through sheer population pressure, rather than at Level 2 territorial expansion.

The internalisation of competition at Level 3 becomes expressed through a differentiation in roles in relation to healthcare and reproduction. If Passive and Active Competition are expressions of k-selection and r-selection, then the logic of this framework is that these become internalised and, by deduction, would have been the reason for the origin of sexual differentiation (in most species: k-selection = females, r-selection = males). In those species, which already express different sexes (i.e. most multicellular organisms), then this internalisation of competition is expressed through increased differentiation of roles in relation to nurture activity. Across many species, which form higher level groups, this involves adding on nurture to the already differentiated roles of foraging and defence: frequently, males take on defence roles, while females focus on nurture of young, both sexes continuing to forage.

LEVEL 3 – PASSIVE COOPERATION

Progression to Level 3 Passive Cooperation takes the division of roles a step further, to full specialisation in relation to nurture – this might be termed division or exchange of nurture (in contrast to that of labour). As with the same effect at Level 2, the outcome is creation of identical agents at inception which grow into differentiated forms as adults. This benefits the whole society but has consequences for the individual agents: they lose the ability to replicate or reproduce successfully alone. Individuals now become reliant on fellow members of their group or society to help them give birth to and then rear off-spring. Social insects take this exchange of nurture to its logical extreme, where through Level 3 indirect reciprocation (or exchange of nurture activity) queens and drones are as reliant on each other for the success of each next generation. Whilst kin selection has been a good model of this effect, the historic focus on the inability of drones to reproduce fails to appreciate that in eusocial colonies the queens are as reliant on the drones for survival and ultimately reproduction of the colony as vice versa.

With full Level 3 Passive Cooperation, a group has now become a new super-organism, capable of generating new whole units – full reproduction, not just replication. Within such new super-groups, agents are now fully dependent on the success of the whole society for their day-to-day survival (Level 1), their on-going growth and security (Level 2), and their health and the propagation of their genes (Level 3). Whole and parts are now entirely mutually dependent for all their needs from Levels 1 to 3. Examples from nature include plants producing seeds, from which whole new plants can grow, and, likewise, insect colonies producing 'seeds', from which whole new colonies can form. All systems up to and including Level 3 are, however, inherently static, rooted to a fixed node of interaction or confined to a territory.

LEVEL 3 – SUMMARY (see Table 5)

Table 5 – Level 3 – consequences of different game strategies

Level 3	**Individual Response**	**Population / Group Behaviour**
Passive Competition	▪ avoiding competition for reproduction ▪ selection for independency (health and nurture) and sequential reproduction (activity specialists in propagating own genes) ▪ biological consequence = extending lifespans	▪ groups or societies without any layering (roaming or territorial)
Active Competition	▪ direct competition for reproduction ▪ increased numbers/frequency of off-spring ▪ selection for biological adaptations to support behavioural changes (increased capability of producing larger numbers of off-spring)	▪ layered groups/societies (layering may be overlaid onto Level 2 hierarchies) ▪ resource partitioning between generations (biological differentiation between young and adults – example of layering) ▪ behaviours such as infanticide likely
Active Cooperation	▪ sharing reproduction opportunities (direct reciprocation in health and nurture) ▪ selection for more reliable reciprocators ▪ no longer competing for number of off-spring	▪ dissolution of layering ▪ emergence of division (exchange) of nurture ▪ managed reproduction of agents giving rise to replicating whole systems
Passive Cooperation	▪ dependent reproducers (no longer capable of reproducing without wider support) ▪ exchanging activities (i.e. some specialising in nurture, others in foraging and defence) ▪ selection for activity generalists (organisms capable of growing into specialist adult roles / forms)	▪ reproducing societies (capable of producing new seeds or equivalent) ▪ formation of nurture supply chains (circulating welfare system) ▪ social good : collective nurture and collective propagation of genes (inclusive fitness)

LEVEL 4 – COMPETITION AND COOPERATION

Within fully evolved Level 3 systems, individual agents (say, the cells or insects) are dependent on being part of the whole group (full plant, full colony) for satisfying their Level 1 to 3 needs. When a new seed is created, it is necessarily displaced from the parent organism, which is already occupying a physical space in a habitat. When that seed arrives in a new location, the whole group is dependent on the constituent agents' ability to source energy and nutrients (eg: the newly formed cells in leaves and roots). If lucky, the new place will be figuratively verdant, and the whole group can thrive and grow into a new organism. But when plants produce millions of seeds and competition ramps up for new static organisms to survive in disparate, less hospitable locations, then new selective pressures come into play.

If a seed were to land in a location, which is not conducive to survival, then it would gain a competitive advantage if it were able to move, to explore and find energy and nutrients in this new place. Survival of the whole consequently becomes dependent on the capacity of the participating agents (say, cells) to communicate to each other where food sources can be found in such unfamiliar terrain and where dangers should be avoided. The component organisms within the group must eventually learn to cooperate. But to start with, they are **competing for spatial information** about sources of energy.

Level 4 Passive Competition manifests as members of a group operating independently, seeking out information about the physical landscape themselves without communicating with each other. This drives competitive spatial intelligence of individuals within the group (both senses and capacity to interpret received information about the environment). In unfamiliar places, such groups may remain static, lose coherence, and enact internally chaotic behaviour … and most likely all die. Level 4 Active Competition manifests as deceit between organisms in the group, representing competitive communication. Internal communities within a group will compete for informational control. This causes the whole to exhibit chaotic movement as one or other internal community asserts itself.

Cooperation arises from members of the group communicating honestly with each other about discovered sources of food within new unfamiliar environments. It is reliant on all members of the group being truthful, pooling and accessing the same information – shared knowledge. To be able to move with intent, they need collectively to formulate decision-making mechanisms (such as voting). Groups, which achieve this, will be more successful than those that remain internally competing for information.

Passive Cooperation takes matters a further step, whereby agents differentiate and become experts in different areas of information gathering and interpretation – each contributing a specialist expertise. The entire group eventually expresses collective intelligence and the ability to move as one with intent across unfamiliar landscapes and survive in new habitats. In the cellular universe, cooperation at Level 4 was expressed through the emergence of different senses and connecting nerves, giving rise to the animal kingdom. And when human tribes learnt to cooperate at Level 4, they gained the freedom to explore the world.

LEVEL 4 – SUMMARY (see Table 6)

Table 6 – Level 4 – consequences of different game strategies

Level 4	Individual Response	Population / Group Behaviour
Passive Competition	▪ independent gatherer of information ▪ selection for increasing spatial intelligence (senses and interpretation of data)	▪ static groups exhibiting internally chaotic behaviour
Active Competition	▪ competing for control and interpretation of information (competitive communication) ▪ more deceitful (behavioural) ▪ selection for biological adaptations to support behavioural changes (improved communication and manipulation of information)	▪ communities (factions) within groups vying for control ▪ chaotic movement of whole group
Active Cooperation	▪ sharing information (pooling knowledge) ▪ selection for more honest communication ▪ competing for influence, not control	▪ coherent group movement ▪ emergence of division (exchange) of information ▪ decision-making processes (eg. voting systems)
Passive Cooperation	▪ agents dependent on others for information ▪ exchanging of information ▪ selection for information generalists (organisms capable of growing into information specialists / communicators)	▪ autonomous societies capable of coherent exploration ▪ formation of information supply chains and cyclic systems to store information ▪ social good : collective intelligence

Summary of Progressive Evolutionary Pathway

Progressing from Level 1 Passive Competition, being a population of competing organisms, up to Level 3 Passive Cooperation, we see the emergence of new static territorial replicating super-agents (entities composed of multiple cooperating originating organisms). The whole is now capable of reproduction. And the original agents are no longer capable of survival other than being a cooperative part of a whole group. Through evolutionary influences along the pathway, such as competitive growth and competitive reproduction, the original organisms will have significantly altered (such as the transformation from prokaryotic to eukaryotic cells).

A full sequence of the pathway is provided in Figure 15 and summarised in Table 7, showing the process starting with a set of competing autonomous organisms leading to a new set of competing autonomous super-agents, which can commence the whole process again, such that:

- prokaryotic cells progress up the interaction layers to become eukaryotic cells in basic multi-cellular entities with all the corresponding emergent differences between these cellular types, including size, asexual/sexual reproduction and so on;
- basic multi-cellular systems progress up the layers to become complex autonomous organisms, expressing a range of sizes and are now fully sexualised;
- complex multi-cellular systems progress up the layers, say from populations of early mammals to form human tribes at the apex; and
- human tribes compete and then cooperate to give form to ever-more complex society.

The consequence of this process is a nested biological system, such as human society composed of humans, themselves composed of cells.

Figure 15 – Overview of whole framework

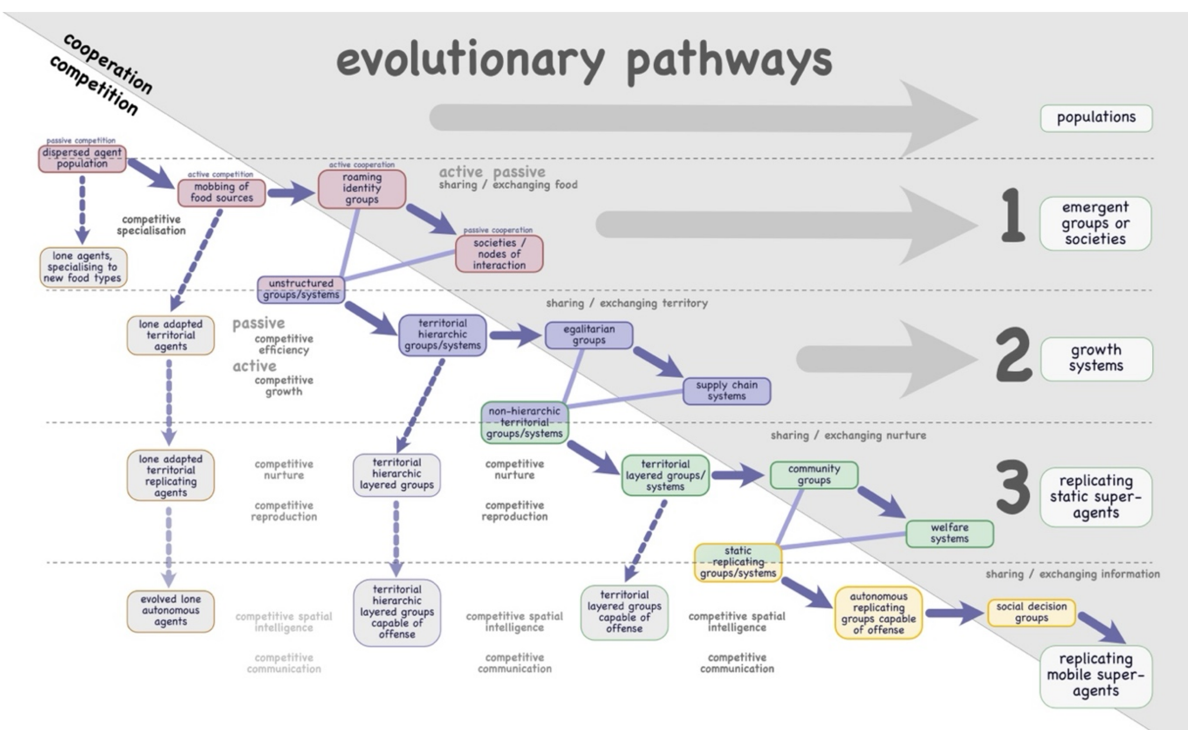


Table 7 – Summary of Emergent System Types

System	Level 1	Level 2	Level 3	Level 4
Passive Competition	population of lone dispersing agents, leading to adaptive radiation	roaming internally (mostly) peaceful unstructured identity groups – selection for increased efficiency	unlayered groups with individual agents nurturing own young	static groups expressing internally chaotic behaviour
Active Competition	population of aggressive agents mobbing of food sources, leading to speciation	territorial hierarchically structured groups – selection for increased growth	layered groups with agents competing for number of off-spring (resource partitioning between generations)	groups expressing externally chaotic behaviour
Active Cooperation	roaming internally (mostly) peaceful unstructured identity groups with leaders and followers	territorial egalitarian groups – emergence of division (exchange) of labour	replicating systems inside which agents provide each other with direct reciprocal nurture	autonomous groups capable of pooling information and taking decisions
Passive Cooperation	emergence of focal points of interaction and increasing omnivory	fixed supply chains and form generalisation, agents capable of growing into differentiated adult organisms	reproducing systems inside which agents are no longer capable of independent reproduction	autonomous societies capable of collective intelligence

Discussion

The framework presented in this paper is a provocative new way of envisaging how evolution can progress for individual species. It is a novel approach, which has not been tried before. Yet, at the same time, this approach can be seen to embrace Darwin's original thesis and is consistent with leading theories on cooperation, such as evolutionary game theory, group theory and kin selection. It can, for instance, explain the differential between group and kin selection (Level 2 to Level 3 systems). And, whilst consistent with the Modern Synthesis, it gives a greater role to organisms, as expressly sought by those promoting the Extended Evolutionary Synthesis.

This approach construes organisms to have a priority set of needs, which define how they act in the real physical world. This leads to interactions between conspecifics, where competition transitions into cooperation to enable organisms to ever better meet their respective needs. But, in so doing, such agents evolve to become ever more reliant on each other for survival. Organisms are seen to compete in four very specific ways: Level 1 – frequency of energy consumption (noting food comes in quanta), Level 2 - rate of intake of energy, Level 3 - total energy, and Level 4 – spatial information. This leads to a layered structure with conspecifics capable of evolving along a pathway of progressively more sophisticated forms of competition and cooperation. Progression up the pathway is, however, ultimately driven by competition within the species – cooperation arising out of competition. And species can evolve forwards and backwards: for example, ursids (all bear species) likely came from cooperative ancestors (hence their omnivory) and reverted to being solitary.

This construct assumes that individual organisms are innately competitive. Even when cooperation emerges, agents remain competitive entities. Erstwhile real competitive behaviours become internalised within cooperative groups and expressed virtually, driving behavioural and cultural changes within groups, which can in turn have biological consequences such as form generalisation. These are the driving forces behind the formation of phenomena such as stem cells and social insect grubs capable of transforming into a variety of mature forms.

Few species have made it all the way up to the top of the cooperative ladder. Many remain competing, becoming ever more specialised or focussing all their energies on maximising growth and reproduction. The higher-level selective pressures for any population of competing agents regardless of whether they have formed any social structuring (groups, etc). But, as shown in Table 1, in the absence of cooperating at a lower level, the higher evolutionary pressures remain significantly moderated (say, Level 2 growth compared to Level 1 food specialisation). Hence, in the right circumstances, a population of lone agents may still grow in size over generations; but this will be at a rate that is far, far slower than if they had already started cooperating at Level 1.

In considering this alternative approach, it is important to remember that in the real world there is a huge amount of noise. Factors such as energy distribution and accessibility, predation, symbiosis with other species and interactions between sexes would in practice hide or distort this idealised construct. But just because so many potential distractions exist does not invalidate the idea that hidden from immediate view there is a very simple framework, an evolutionary pathway, up which species have the potential to climb, eventually leading to ourselves. If this approach is valid, then it suggests the reason for our own rapid evolution is that through intense (probably quite brutal) competition *we made ourselves*. Further, if this is valid, then human tribes must have reached Level 4 cooperation for them to have gained the autonomy to explore the world beyond the shores of Africa.

Is this the type of construct that many have been searching for – perhaps. It most certainly needs refinement and testing. But it hopefully provides an initial skeleton for a new way of looking at social evolution, allowing the study of species' evolution to progress from description and retrodiction to explanation and prediction. If found to be valid, then it has the scope for application beyond the biological sciences.

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Tables

Figures

Figure 14 – Evolutionary Pathway – Level 2 to Level 3 Systems

Figure 15 – Evolutionary Pathways