Does the evolution of division of labour require accelerating returns from individual specialisation?

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Abstract

Recent theory has overturned the assumption that accelerating returns from individual specialisation are required to favour the evolution of division of labour. Yanni et al. (2020) showed that topologically constrained groups, where cells cooperate with only direct neighbours such as for filaments or branching growths, can evolve a reproductive division of labour even with diminishing returns from individual specialisation. We developed a conceptual framework and specific models to investigate the factors that can favour the initial evolution of reproductive division of labour. We found that selection for division of labour in topologically constrained groups: (1) is not a single mechanism to favour division of labour – depending upon details of the group structure, division of labour can be favoured for different reasons; (2) always involves an efficiency benefit at the level of group fitness; and (3) requires a mechanism of coordination to determine which individuals perform which tasks. Given that such coordination is unlikely to evolve before division of labour, this limits the extent to which topological constraints could have favoured the initial evolution of division of labour. We conclude by suggesting experimental designs that could determine why division of labour is favoured in the natural world.

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Introduction

Division of labour, where cooperating individuals specialise to carry out distinct tasks, plays a key role at all levels of biology (Bourke, 2011; Queller, 1997; Maynard Smith & Szathmáry, 1995; West et al., 2015). Cells are built by genes carrying out different functions (Bourke, 2011; Levin & West, 2017). In clonal groups of bacteria, cells specialise to produce and secrete different factors that facilitate growth (Dragoš et al., 2018a; Veening et al., 2008; West & Cooper, 2016). Pathogens rely on division of labour for protection from the host immune response and competitors (Ackermann et al., 2008; Diard et al., 2013). Multicellular organisms are composed of reproductive germ cells and sterile somatic cells that are not passed to the next generation (Bourke, 2011; Maynard Smith & Szathmáry, 1995). The ecological dominance of the social insects arises from division of labour between queens and the different types of workers (castes) (Oster & Wilson, 1978; Wilson, 1978).

It has long been established that the evolution of division of labour requires an efficiency benefit from individual specialisation (Figure 1A & 1B for reproductive division of labour) (Bourke, 2011; Cooper & West, 2018; Ispolatov et al., 2012; Michod, 2006; Oster & Wilson, 1978; Schiessl et al., 2019; Smith, 1776; Maynard Smith & Szathmáry, 1995; Solari et al., 2013). In particular, that there is an accelerating (convex) return when individuals commit more effort to a particular task, such that twice the investment more than doubles the return (Bourke, 2011; Cooper & West, 2018; Ispolatov et al., 2012; Michod, 2006; Solari et al., 2013). An accelerating return from individual investment can exist for several reasons. A task could become more effective as more effort is put into it, or it could incur diminishing costs. This could occur if there are larger upfront costs from performing a task. For instance, any reproduction by a cell in Volvocine groups first requires individual growth to the size of a

daughter colony (Michod, 2006). Alternatively, there could be a disruptive cost to carrying out multiple tasks at the same time, if the tasks don't mix well. For instance, in cyanobacteria the enzymes that fix environmental nitrogen are degraded by oxygen, a bi-product of photosynthesis (Flores & Herrero, 2010).

Figure 1: Division of labour is favoured by accelerating returns from individual specialisation. (A) Theory has shown that either a linear or diminishing return from more cooperation (or reproduction) favours uniform cooperation, with all individuals investing the same amount of effort into cooperation and reproduction (i.e. no division of labour) (Cooper & West, 2018; Michod, 2006; Schiessl et al., 2019). (B) In contrast, an accelerating return from more cooperation (or reproduction) favours reproductive division of labour, with some individuals specialising in high levels of cooperation (helpers) and others in low levels of cooperation (reproductives) (Cooper & West, 2018; Michod, 2006; Schiessl et al., 2019).

In contrast, Yanni et al. found that division of labour between helpers and reproductives can sometimes be favoured even when there are diminishing (concave) returns from individual specialisation (Yanni et al., 2020). Specifically, reproductive division of labour could arise in topologically constrained groups—where each cell in a spatially structured group shares cooperative benefits with only their direct neighbours (Staps & Tarnita, 2020; Yanni et al., 2020). Their analyses suggested that this is particularly likely to occur in sparsely structured groups, where cells have a small number of neighbours (Yanni et al., 2020). This is a novel result. Diminishing returns means that specialised individuals are inefficient, and earlier work suggested that division of labour could not be favoured in this situation (Figure 1A) (Cooper & West, 2018; Michod, 2006; Schiessl et al., 2019). Consequently, this result has the potential to overturn our understanding of the factors that favour the evolution of division of labour.

However, there are several issues that still need to be resolved with how topological constraints can favour division of labour. Why exactly do the predictions of this new theory differ from previous theory? Are special group structures the only way to alter the predictions of the previous theory, or is this an example of a more general phenomenon (Rueffler et al., 2012)? Do these findings rely upon implicit assumptions, that may not be reasonable during the initial evolution of division of labour? Answering these questions is not only of theoretical importance: it is also key for planning future empirical studies. Quantifying the shape of the returns from individual specialisation has been assumed to be a fundamental step in determining why division of labour was favoured in some species, but not others (Diard et al., 2013; Dragoš et al., 2018a; Flores & Herrero, 2010; Koufopanou, 2002; Mridha & Kummerli, 2021; Strassmann et al., 2000; Veening et al., 2008).

We use the methodology developed by Rueffler et al. to derive the general conditions that favour the initial evolution of reproductive division of labour between helpers and reproductives (Rueffler et al., 2012). We then use this framework to examine when and why topological constraints can favour division of labour. More specifically, we determine the ultimate cause of division of labour in specific topologically constrained groups, such as filaments and branching growths, as well as in a general analysis of arbitrary group structures. We then ask whether division of labour without an accelerating return from individual specialisation could arise in groups without topological constraints. To test our hypothesis that between-individual coordination is required for division of labour in these cases, we re-examine our models while assuming that cells adopt helper and reproductive roles randomly (no coordination). We finish by suggesting experimental designs for determining why division of labour has evolved in specific species.

Results

General invasion analysis

We follow Yanni et. al, and a number of previous models, by assuming that individual fitness is the product of individual viability, which is the chance of surviving to maturity, and individual fecundity, which is proportional to the number of offspring if the individual reaches maturity (Cooper & West, 2018; Michod, 2006; Yanni et al., 2020). We examine the specific case of reproductive division of labour between helpers and reproductives, where helpers are more cooperative, contributing to a higher viability for group members, and reproductives are less cooperative, contributing to higher individual fecundity.

We consider an initial population of clonal groups each containing n individuals, in which all individuals cooperate at the Evolutionarily Stable (ES) level (z^*), which is the level that cannot

be outcompeted by a mutant strain that uses a different level of uniform cooperation across the group (Maynard Smith, 1982). We then ask when this population of uniform cooperators can be invaded by a mutant strain that employs a reproductive division of labour.

Without loss of generality, we assume that the mutant strain is composed of n_h helpers that invest z_h into cooperation and n_r reproductives that invest z_r into cooperation (where $n_h + n_r = n$ and $z_h > z_r$). We set individual fitness as the product of individual fecundity, $F > 0$, and individual viability, where helpers and reproductives may in principle have different viability functions, $V_h > 0$ and $V_r > 0$ (but see appendix C.2.) (Michod, 2006; Yanni et al., 2020). The fitness of the clonal group is given by the sum of individual fitness:

$$W(z_h, z_r) = n_h F(z_h) V_h(z_r, z_h) + n_r F(z_r) V_r(z_r, z_h), \quad (1)$$

where the first term on the right-hand side is the total fitness of the prospective helpers and the second term on the right-hand side is the total fitness of the prospective reproductives.

Fecundity is determined by an individual's investment in cooperation ($F = F(z)$, where z is the focal individual's level of cooperation) and viability is determined by the level of cooperation at the level of the group ($V_h = V_h(z_h, z_r)$ and $V_r = V_r(z_h, z_r)$). We assume that there is a trade-off between fecundity and viability such that higher individual cooperation leads to lower individual fecundity ($F'(z) < 0$), but that more cooperation leads to a higher viability for all individuals (i.e. $V_h^{z_h}, V_h^{z_r}, V_r^{z_h}, V_r^{z_r} > 0$, where superscripts denote partial derivatives).

We determine the invadability conditions that favour reproductive division of labour by applying the general approach of Rueffler et al. (Rueffler et al., 2012). The key step is to

approximate the relative fitness of a reproductive division of labour mutant by taking a second-order Taylor expansion of fitness, centred on the resident strategy of uniform cooperation, z^* :

$$W(z^* + \Delta z_h, z^* + \Delta z_r) - W(z^*, z^*) \approx$$

$$W^{z_h} \Delta z_h + W^{z_r} \Delta z_r + \frac{1}{2} W^{z_h z_h} \Delta z_h^2 + \frac{1}{2} W^{z_r z_r} \Delta z_r^2 + W^{z_h z_r} \Delta z_h \Delta z_r,$$

(2a) (2b) (2c) (2d) (2e)

where $\Delta z_h > \Delta z_r$ captures the change in the level of cooperation for mutant helpers and reproductives, respectively, which we assume are small in magnitude. The superscripts represent first and second order partial derivatives, where all partial derivatives are evaluated at the resident strategy of uniform cooperation ($z_h = z_r = z^*$). If a mutant strain exists such that Equation 2 is positive ($W(z^* + \Delta z_h, z^* + \Delta z_r) > W(z^*, z^*)$), then division of labour between helpers and reproductives is favoured to evolve. Conversely, if for all possible mutant strains, Equation 2 is negative ($W(z^*, z^*) > W(z^* + \Delta z_h, z^* + \Delta z_r)$), then uniform cooperation is evolutionarily stable.

The three pathways to division of labour

We found that reproductive division of labour could be favoured for three distinct reasons, corresponding to different subsets of terms on the right-hand side of Equation 2. Our results for reproductive division of labour, where fitness is partitioned as the product of fecundity and viability, align with those found by Rueffler et al. for division of labour more generally (Rueffler et al., 2012). We now go through these three distinct scenarios.

Scenario 1: Accelerating returns from individual specialisation

The first and most studied scenario that can favour division of labour is when there are accelerating returns from individual specialisation. This occurs if there is an accelerating fitness

return from either helper specialisation in cooperation and / or reproductive specialisation in fecundity (Figure 1) (Cooper & West, 2018; Michod, 2006; Oster & Wilson, 1978).

Mathematically, this scenario is a consequence of the third and fourth terms of the Taylor expansion (2c & 2d), which capture the second-order fitness effect of a small, unilateral change in cooperation by either prospective helpers or reproductives, respectively. Division of labour is favoured to evolve whenever at least one of 2c and 2d is greater than zero ($W^{zh} > 0$ or $W^{zr} > 0$), and where we have assumed that the first two terms are both zero ($W^{zh} = 0$ and $W^{zr} = 0$; see between-individual differences below; Figure 2A). In either scenario, an efficiency benefit to group fitness arises from individual specialisation because the more exclusive effort that each individual puts into a task, the better they can perform that task. Rueffler et al. termed these kinds of scenario as ‘accelerating performance functions’ (Rueffler et al., 2012).

Scenario 2: Between-individual differences

The second scenario that can favour reproductive division of labour is when there are pre-existing differences between individuals in the group, such that some individuals are predisposed to one task or the other. For example, if some individuals can secure larger viability benefits for the group at the same fecundity cost as others (Figure 2B).

Figure 2: Division of labour is favoured by between-individual differences. Division of labour is favoured if some individuals are predisposed to being reproductives or helpers. (A) In the absence of another mechanism, if there are no differences between individuals (black and grey lines), then division of labour is not favoured. (B) If some individuals can produce larger viability benefits than others (black line), or if some individuals can access greater fecundity benefits than others (grey line), then this predisposition favours division of labour.

This scenario is captured by the first two terms of the Taylor expansion (2a and 2b), which are the first-order fitness effects from a small, unilateral change in the level of cooperation by prospective helpers or reproductives. If the direct fitness effects are non-zero (positive or negative) at the resident strategy of uniform cooperation ($W^{zh} \neq 0$ or $W^{zr} \neq 0$), then division of labour can invade independently of any higher-order effects (the remaining terms in Equation 2).

We term this scenario ‘between-individual differences’ because it requires that there is pre-existing phenotypic or environmental variation between individuals in the group. For the within-species case, ancestral groups are usually composed of clonal or highly related individuals, who will be phenotypically similar or identical. Consequently, this mechanism could be less important for the division of labour except when there are consistent differences in the microenvironment experienced by different individuals (Tverskoi et al., 2018; Tverskoi & Gavrillets, 2021). In contrast, this scenario is likely to be widespread in the evolution of non-reproductive division of labour between species, such as for mutualisms or symbioses (Kiers et al., 2011; Rueffler et al., 2012; Wyatt et al., 2014). Individuals of different species often differ in their abilities to perform certain tasks (Kiers et al., 2011). Rueffler et al. termed this scenario ‘positional’, but we avoid that term to prevent confusion with topological position (Rueffler et al., 2012).

Between-individual differences provides a first-order fitness benefit to dividing labour, and so it does not matter whether the subsequent benefits of increased cooperation or fecundity are accelerating or diminishing (Figure 1), so long as these benefits are different for different individuals (Figure 2). When some individuals are predisposed to being either helpers or reproductives, then individual specialisation provides an efficiency benefit to group fitness by capitalising on these inherent differences.

Scenario 3: Reciprocal specialisation

The final scenario that can favour division of labour is when reciprocal specialisation by both helpers and reproductives provides a fitness benefit to the group (Figure 3). This scenario requires two key conditions. First, simultaneous specialisation, where some individuals invest more in cooperation (more viability benefits for the group), and others invest less in

cooperation (greater individual fecundity; but see below). Second, this reciprocal specialisation must provide a group-level fitness benefit, because the increased benefits of cooperation are preferentially directed towards reproductives.

Figure 3: Division of labour is favoured by reciprocal specialisation. We assume that there are diminishing returns from specialisation in either viability or fecundity (Figure 1A). (A) In this case, a unilateral increase in cooperation by helpers or a unilateral decrease in cooperation by reproductives leads to a diminishing fitness benefits to the group, which favours uniform cooperation (no division of labour). (B) In contrast, a reciprocal increase in cooperation by helpers (more viability benefits provided by helpers) and a decrease in cooperation by reproductives (larger reproductive fecundity) can produce an accelerating return to the fitness of the group if the benefits of increased cooperation are preferentially directed to reproductives. Thus, reciprocal specialisation can still favour division of labour, even though the returns from individual specialisation are diminishing. In the middle plots of (A) and (B), only the shape of the benefits from increased specialisation are plotted.

Mathematically, this scenario involves the last term of the Taylor expansion ($2e; W^{z_h z_r} \Delta z_h \Delta z_r$). This term is generated by a between-individual, second-order fitness effect, capturing how increased investment in viability by some individuals affects the returns from increased investment in fecundity by others, and vice-versa. Rueffler et al. referred to this as a ‘synergistic benefit’ to division of labour (Queller, 1985, 2011; Rueffler et al., 2012).

Critically, this scenario still involves an efficiency benefit to specialisation, but at the level of group fitness rather than in each fitness component separately (appendix C.1). By this we mean that there is an accelerating fitness benefit to the group when helpers and reproductives reciprocally specialise, leading to a higher group fitness than in groups with uniform cooperation (generalists). This occurs if the increased help given to reproductives is sufficiently amplified by the increased fecundity of reproductives (Yanni et al., 2020). This synergistic efficiency benefit can favour division of labour even if there are diminishing returns from individual specialisation.

Division of labour by reciprocal specialisation can also evolve without a joint mutation in the level of cooperation of both helpers and reproductives (no simultaneous specialisation). In this case, the chance invasion (to fixation) of a slightly deleterious mutant that specialises in only one phenotype (Figure 5A) can destabilise uniform cooperation, creating a selection pressure for the other phenotype to also specialise that is greater than the selection pressure to purge the initial mutant. In this scenario, it is nevertheless the synergistic benefit from reciprocal specialisation that makes division of labour more efficient.

Topological constraints in the general framework

Our above analysis has shown that reproductive division of labour can be favoured for three reasons: (1) accelerating returns make individual specialisation more efficient; (2) between-individual differences make individual specialisation more efficient; or (3) there is a synergistic efficiency benefit from reciprocal specialisation. These results agree with previous analyses by Rueffler et al. (Rueffler et al., 2012).

We now use this framework to examine how and why topological constraints can favour division of labour in the absence of an accelerating return from individual specialisation (i.e. when scenario 1 does not hold). We ask three questions. First, can topological constraints favour division of labour by between-individual differences (scenario 2), and / or by reciprocal specialisation (scenario 3)? Second, are topological constraints the only way to evolve a division of labour without an accelerating return from individual specialisation? Third, does the evolution of division of labour by between-individual differences (scenario 2) and reciprocal specialisation (scenario 3) require coordination between individuals to determine which cells become helpers or reproductives?

Question 1: How do topological constraints favour division of labour?

We consider two spatial models, based on the group structures proposed by Yanni et al., to examine whether topologically constrained groups favour division of labour by: (a) between-individual differences; and / or (b) reciprocal specialisation (Yanni et al., 2020).

(a) Can topological constraints lead to division of labour by between-individual differences?

Consider a group in which cells alternately have either two or three neighbours, in a branching structure (Figure 4A). Such a group structure might have occurred for some early forms of multicellular life (Yanni et al., 2020). We term cells with three neighbours “node” cells and

cells with two neighbours “edge” cells. We assume that cells investing an amount z into cooperation produce an amount $H(z)$ of a public good. We assume non-accelerating returns from individual specialisation (i.e. $H''(z) \leq 0$ or $F''(z) \leq 0$). The cell keeps a fraction $1 - \lambda$ of the public good that it produces, and the remaining fraction λ is shared equally between its direct neighbours (the “shareability” of cooperation: $0 < \lambda \leq 1$). We assume that the viability of a cell is equal to the sum of the public good that it absorbs.

For this model, we find that for all social traits ($\lambda > 0$), reproductive division of labour by between-individual differences can evolve (Figure 4D; appendix A.1). This occurs because different cells have different viability-fecundity trade-offs depending on their position in the group. Edge cells receive relatively less public good from their (fewer) neighbours, and so pay a smaller opportunity cost from decreased fecundity (increased cooperation). In contrast, node cells receive relatively more public good from their (more numerous) neighbours, and so pay a larger opportunity cost from decreased fecundity (increased cooperation). Consequently, this between-cell difference favours node cells to specialise in fecundity (reproductives) and edge cells to specialise in increased cooperation (helpers). Importantly, because this pathway to division of labour is driven entirely by a first-order effect (2a & 2b), it does not require a second-order efficiency benefit from specialisation (2c, 2d or 2e).

More generally, a formal analysis of arbitrary group structures reveals that division of labour by between-individual differences can always evolve whenever the number of neighbours varies for different cells in the group (appendix A.2).

(b) Can topological constraints lead to division of labour by reciprocal specialisation?

Consider a one-dimensional chain of cells, as examined by Yanni et al. Chains are found in species like cyanobacteria that form filaments of cells, and such structures might have been important at the onset of the evolution of multicellularity (Figure 4B) (Yanni et al., 2020). We assume arbitrarily that “odd” cells along the filament are putative helpers and “even” cells are putative reproductives. We otherwise make the same assumptions as for the branching structure model: there is a non-accelerating return from individual specialisation (i.e. $H''(z) \leq 0$ or $F''(z) \leq 0$), and the cell keeps a fraction $1 - \lambda$ of the public good that it produces, with the remaining fraction λ being shared equally by its direct neighbours.

If the amount of public good shared with neighbours is sufficiently large (high λ), then we find that division of labour via reciprocal specialisation can evolve (Figure 4E; appendix A. 3). For instance, in the case of linear fecundity and public good returns ($H''(z) = F''(z) = 0$), division of labour by reciprocal specialisation can evolve if helpers share more of the public good that they produce with their neighbours than they keep for themselves ($\lambda > \frac{1}{2}$). If there are diminishing returns from specialisation ($H''(z) < 0$ or $F''(z) < 0$), then division of labour can still be favoured but then the amount of the public good preferentially shared with neighbours must be even greater still (higher λ ; Figure 4E).

In appendix A.5, we show with a formal analysis of arbitrary group structures that division of labour can be favoured due to reciprocal specialisation if:

$$\lambda\mu > d \quad (3)$$

where λ is the shareability of cooperation, μ is a measure of how easily the group can be “bi-partitioned”, and d is the average number of neighbours across all cells. Thus, reciprocal specialisation can favour division of labour if: (1) groups are more sparse (low d); (2) groups are structured such that helpers can be neighbours with reproductives more than with other helpers, and vice-versa (high μ); and/or (3) when the benefits of cooperation are preferentially shared with neighbours (high λ). In combination, these three factors amplify the synergistic benefits of reciprocal helper and reproductive specialisation, which can produce an accelerating fitness return for the group, even when there are non-accelerating returns from individual specialisation (appendix C. 1).

If one or two of these factors are particularly favourable for reciprocal specialisation, then the condition(s) on the remaining factor(s) can be relaxed. For instance, cells in a filament have only 2 neighbours ($d = 2$), and the potential alternation of helpers and reproductives in the filament means that helpers can share their cooperative public goods with reproductives exclusively (maximal μ). Consequently, reciprocal specialisation is possible even when the shareability of cooperation is reasonably low (e.g. $\lambda > \frac{1}{2}$ for linear benefits).

To conclude, topological constraints are not a single explanation for division of labour, in that they can favour division of labour for two different biological reasons. Different group structures can lead to either between-individual differences favouring division of labour (scenario 2), or reciprocal specialisation favouring division of labour (scenario 3). In all cases, there is an efficiency benefit from specialisation at the level of group fitness even if the returns from individual specialisation are non-accelerating.

Figure 4: The impact of topological constraints on the division of labour. We consider more specific models, including: (A) a branching group; (B) a filament; and (C) a well-mixed group. (D) In a branching group structure, division of labour in the absence of accelerating returns from specialisation can be favoured by between-individual differences whenever the benefits of cooperation are shared ($\lambda > 0$). (E) In a filament structure, division of labour in the absence of accelerating returns from individual specialisation can be favoured by reciprocal specialisation when cells share a sufficient majority of the public good they produce with neighbours (e.g. when linear returns: $\lambda > \frac{1}{2}$). (F) In a well-mixed group, division of labour in the absence of accelerating returns from specialisation can be favoured by reciprocal specialisation if cells share an even larger proportion of the public good they produce with neighbours (e.g. when linear returns: $\lambda > \frac{n-1}{n}$). In (D), (E) and (F), we have assumed a linear return from fecundity specialisation, $F(x) = 1 - x$, and a potentially non-linear return from investment in cooperation, $H(x) = x^\alpha$, where α controls the shape of the return.

Question 2: Are topological constraints required for division of labour without accelerating returns from individual specialisation?

We considered a well-mixed social group of n cells, where all cells share the benefits of cooperation with one another, and so there are no topological constraints (Figure 4C). We then examined whether division of labour could be favoured by: (a) between individual differences; and / or (b) reciprocal specialisation. In both cases, we assume that when a cell invests z into cooperation, it produces an amount $H(z)$ of a public good. A cell keeps a fraction $1 - \lambda$ of the public good that it produces and the remaining fraction λ is shared by the rest of the social group members equally. We again consider the case where there is a non-accelerating return from individual specialisation ($H(z)'' \leq 0$; $F''(z) \leq 0$).

(a) Can between-individual differences favour division of labour without a topological constraint?

In the well-mixed group of identical cells, we find that division of labour cannot arise by between individual differences (appendix A. 4). This is because all cells have the same number of neighbours, which we have shown more generally can never produce between-individual differences. This prediction could be violated if one of our assumptions do not hold: for instance, if there are consistent differences in the microenvironment that predispose some cells to one task or the other (Tverskoi et al., 2018; Tverskoi & Gavrillets, 2021; Yanni et al., 2020).

(b) Can reciprocal specialisation favour division of labour without a topological constraint?

In the well-mixed group of identical cells, if the amount of public good shared with neighbours is sufficiently large (high λ), then we find that division of labour via reciprocal specialisation can evolve (Figure 4F; appendix A. 4.). If there are linear returns from increased specialisation ($H''(z) = F''(z) = 0$), then division of labour can evolve when the public good produced by an individual benefits an average group-member more than the producer ($\lambda > \frac{n-1}{n}$; Figure 5F).

These results are like those found for a filament of cells (Figure 4E). In both cases, more

generous sharing (higher λ) means that the synergistic benefits of reciprocal specialisation can be great enough to compensate for the non-accelerating returns from individual specialisation. In well-mixed groups, very generous sharing ($\lambda \approx 1$) also compensates for the fact that helpers are neighbours with all other helpers (no sparsity and minimally “bi-partionable”).

To conclude, the well-mixed model shows that a topological constraint is not required for the evolution of division of labour with non-accelerating returns from individual specialisation. This is in direct contradiction to the results of Yanni et. al., in which a helper was never allowed to benefit less than any of its neighbours from its own public good production ($\lambda \leq \frac{n-1}{n}$) (Yanni et al., 2020). In our model with a group of well-mixed cells, division of labour is favoured because it provides an efficiency benefit at the group level, via reciprocal specialisation (scenario 3), in an analogous way to our model with a one-dimensional chain of cells (question 1b).

Question 3: Is coordination required to favour division of labour without accelerating returns from individual specialisation?

We hypothesised that the benefits of between-individual differences (scenario 2) or reciprocal specialisation (scenario 3) rely on the implicit assumption that cells are coordinating which individuals specialise to become reproductive and helpers. This matters because mechanisms for coordinating division of labour, such as between cell signalling, might not be expected to exist before division of labour has evolved. Consequently, if coordination was required, then this could limit the extent to which topological constraints favour the initial evolution of division of labour.

We investigated this hypothesis by repeating our above analyses, while assuming that cells do not have access to information that allows them to coordinate their phenotypes. Specifically, cells do not know if they are “odd” or “even”, or if they are “edge” or “node”. We assumed instead that a reproductive division of labour mutant induces each cell in the group to adopt the role of a helper or reproductive with a uniform probability (random specialisation). Random specialisation has been observed in a number of microbes (Ackermann et al., 2008; Diard et al., 2013; Veening et al., 2008). For filaments, branching group structures, and well-mixed groups, we found that division of labour can no longer evolve with non-accelerating returns from individual specialisation (appendices B. 1. and B 2.). In appendix B. 3, we have shown that this result holds for any group structure.

Consequently, for division of labour to evolve with non-accelerating returns from individual specialisation, there must exist some mechanism to coordinate which cells specialise to perform which tasks. A clear example of coordinated division of labour in topologically constrained groups is the use of between-cell signalling in some cyanobacteria filaments to determine which cells become nitrogen fixing heterocysts (Flores & Herrero, 2010; Meeks & Elhai, 2002). However, a signal to coordinate distinct phenotypes is unlikely to exist prior to division of labour, and so a topological constraint is less likely to have favoured the initial evolution of division of labour in cyanobacteria. Instead, division of labour could have been favoured by an accelerating return from individual specialisation (scenario 1), with coordination only evolving subsequently. Empirically, an accelerating return seems likely, as the key tasks performed by reproductives and helpers do not mix well (photosynthesis and nitrogen fixation) (Flores & Herrero, 2010; Meeks & Elhai, 2002).

These analyses do not suggest that topological constraints could never favour the initial evolution of division of labour. As an alternative to signalling, a pre-existing cue could allow division of labour to initially evolve with a metabolically cheaper form of coordination. For example, phenotype could be determined in response to the number of neighbours or the local concentration of some resource. However, the biological plausibility of any mechanism based on pre-existing cues would need to be explicitly justified and modelled on a case-by-case basis (Duarte et al., 2011). This would include modelling the metabolic cost and effectiveness of any coordination mechanism (Cooper et al., 2020; Duarte et al., 2012; Liu et al., n.d.). Empirically, while between-cell coordination has evolved in several labour-dividing microbial species, further studies—such as ancestral-state reconstructions—are needed to show whether coordination preceded division of labour in individual species.

Distinguishing the ultimate causes of division of labour in the wild

How can we distinguish empirically which of the different scenarios favoured real world examples of division of labour (Figure 5)? We suggest experimental designs for microbial systems, where mixtures of helper and reproductive cells are grown together, and which make use of methods to genetically manipulate and measure the relative levels of cooperation and reproduction of each phenotype (Ackermann et al., 2008; Diard et al., 2013; Dragoš et al., 2018a; Dragoš et al., 2018b; Mavridou et al., 2018; Mridha & Kummerli, 2021; van Gestel et al., 2015). These are rough suggestions for the kind of experiments required, as details and possibilities will vary system from system, depending upon factors such as the degree of specialisation, the mechanism by which labour is divided, and what manipulations are possible. In addition, these experiments would need to follow from key first steps, such as demonstrating division of labour and a trade-off between reproduction and cooperation (Diard et al., 2013; Dragoš et al., 2018a; Dragoš et al., 2018b; Veening et al., 2008; Zhang et al., 2020).

A) Accelerating returns from individual specialisation

B) Between-individual differences

C) Reciprocal specialisation

Figure 5: Experimental guidelines to distinguish the causes of division of labour. (A) To test whether division of labour is favoured by an accelerating return from individual specialisation, we must separately determine whether an increase in helper cooperation or a decrease in reproductive cooperation leads to an accelerating increase in group fitness. (B) To

test whether division of labour is favoured by between-individual differences we must determine whether an increase in cooperation by helpers produces a different group fitness benefit than an increase in cooperation by reproductives. (C) To test whether division of labour is favoured by reciprocal specialisation, we must determine whether there exists at least one relative degree of helper-to-reproductive specialisation for which group fitness is greater than the fitness of uniform cooperation.

Testing for between-individual differences (scenario 2): In some treatments, vary the level of cooperation of helpers (Figure 5B top-left). In other treatments vary the level of cooperation of reproductives (Figure 5B bottom-left). If division of labour evolves in this system by between-individual differences, then we should observe that group fitness varies differently depending on whether it is helpers or reproductives that are cooperating at a higher rate (Figure 5B right).

Testing for reciprocal specialisation (scenario 3): Use a classic $N \times N$ factorial experiment where the level of cooperation performed by helpers, and the level of reproduction performed by reproductives are both varied (Figure 5C left). Division of labour is favoured by reciprocal specialisation if there is a significant interaction term between these two factors, with at least one treatment that produces a group fitness larger than that for uniformly cooperating cells (Figure 5C right).

Conclusion

Division of labour can be favoured to evolve without accelerating returns from individual specialisation. Nevertheless, for this to occur requires: (a) between-individual differences in task-efficiency or synergistic benefits from reciprocal specialisation; and (b) a mechanism to coordinate which individuals perform which tasks. In contrast, accelerating returns can favour division of labour without a mechanism to coordinate task allocation, possibly making it more

512 likely to favour the initial evolution of division of labour. Ultimately, determining the relative
513 importance of these different pathways to division of labour is an empirical question, requiring
514 experimental studies of the type we have outlined above.

515

516 Materials and Methods

517 Resident strategy of uniform cooperation

518 We start by solving for the ESS strategy where both types of individuals invest the same amount
 519 in cooperation ($z_h = z_r = z$; uniform cooperation). This is the level of uniform investment in
 520 cooperation, z^* , for which there is no selection for a uniform change in the amount of cooper-
 521 ation by all individuals in the group:

$$\left. \frac{\partial W(z, z)}{\partial z} \right|_{z=z^*} = 0.$$

522 More explicitly, we can write this as:

$$\begin{aligned} & n_h F V_h \left(\frac{F'}{F} + \frac{n_h V_h^{z_h} + n_r V_r^{z_h}}{n_h V_h} \right) \Big|_{z_h=z_r=z^*} \\ & + n_r F V_r \left(\frac{F'}{F} + \frac{n_h V_h^{z_r} + n_r V_r^{z_r}}{n_r V_r} \right) \Big|_{z_h=z_r=z^*} = 0, \end{aligned} \quad (4)$$

523 where we have suppressed the functional dependencies for ease of presentation. The first term
 524 gives the group fitness change due to a marginal increase in “helper” cooperation, and the
 525 second term gives the group fitness change due to a marginal increase in “reproductive” coop-
 526 eration. So, at the uniform strategy, z^* , any increase in the fitness caused by the increased co-
 527 operation of one subgroup of the population is balanced by a commensurate decrease in fitness
 528 caused by the same increase in cooperation for the other subgroup ($\partial W(z_h, z_r)/\partial z_h|_{z_h=z_r=z^*} =$
 529 $-\partial W(z_h, z_r)/\partial z_r|_{z_h=z_r=z^*}$).

530 The constrained optimum, $(z_h, z_r) = (z^*, z^*)$, computed using Equation 4, does not nec-
 531 essarily correspond to a critical point of W : i.e. the first derivatives $\partial_{z_h} W$ and $\partial_{z_r} W$ might not
 532 vanish at this point. However, if the functions V_h and V_r are *symmetrical*, in the sense that

$$n_h V_h(z_h, z_r) = n_r V_r(z_r, z_h), \quad (5)$$

533 then the fitness function satisfies $W(z_h, z_r) = W(z_r, z_h)$, and it can be seen that this implies

534 that the point $(z_h, z_r) = (z^*, z^*)$ is actually a critical point of $W(z_h, z_r)$.

535 Division of labour by between-individual differences

536 Division of labour by between-individual differences occurs if either of the first two terms of
537 the Taylor expansion (Equation 2) is non-zero ($W^{z_h} \neq 0$ or $W^{z_r} \neq 0$). In this case, directional
538 selection will increase or decrease the level of cooperation of one of the individual types. We
539 give here the associated partial differentials of fitness (Equation 1):

$$\left. \frac{\partial W}{\partial z_h} \right|_{z_h=z_r=z^*} = n_h F' V_h + n_h F V_h^{z_h} + n_r F V_r^{z_h}, \quad (6)$$

$$\left. \frac{\partial W}{\partial z_r} \right|_{z_h=z_r=z^*} = n_r F' V_r + n_h F V_h^{z_r} + n_r F V_r^{z_r}. \quad (7)$$

540 These expressions capture the fitness consequences of a marginal increase in cooperation by
541 helpers and reproductives, respectively. The first term of each captures the fecundity cost to
542 own type of producing more public good, whereas the second term and third term are the via-
543 bility benefits that accrue to both types from this increased cooperation. If directional selection
544 in both traits is zero ($\partial W / \partial z_h|_{z^*} = 0$ and $\partial W / \partial z_r|_{z^*} = 0$), then $z_h = z_r = z^*$ is a critical
545 point, and Equations 6 and 7 imply that

$$\left. \frac{F'}{F} \right|_{z_h=z_r=z^*} = - \frac{n_h V_h^{z_h} + n_r V_r^{z_h}}{n_h V_h} \Big|_{z_h=z_r=z^*}, \quad (8)$$

$$\left. \frac{F'}{F} \right|_{z_h=z_r=z^*} = - \frac{n_h V_h^{z_r} + n_r V_r^{z_r}}{n_r V_r} \Big|_{z_h=z_r=z^*}. \quad (9)$$

546 These equations mean that, if $z_h = z_r = z^*$ is a critical point, then any marginal viability
547 benefit to the group of increased cooperation by one subgroup is cancelled by the fecundity
548 cost to that same subgroup. Moreover, Equations 8 and 9 together imply that

$$\frac{n_h V_h^{z_h} + n_r V_r^{z_h}}{n_h V_h} \Big|_{z_h=z_r=z^*} = \frac{n_h V_h^{z_r} + n_r V_r^{z_r}}{n_r V_r} \Big|_{z_h=z_r=z^*}, \quad (10)$$

549 If this equation does not hold, then $z_h = z_r = z^*$ is not a critical point: i.e. there is a difference
550 in the viability-fecundity tradeoffs between subgroups such that some individuals (without loss
551 of generality, helpers) can secure larger benefits for the group at the same fecundity cost as
552 others (reproductives). This gives our first condition for division of labour being able to evolve:

553 **The between-individual differences condition for division of labour**

$$\left. \frac{n_h V_h^{z_h} + n_r V_r^{z_h}}{n_h V_h} \right|_{z_h=z_r=z^*} > \left. \frac{n_h V_h^{z_r} + n_r V_r^{z_r}}{n_r V_r} \right|_{z_h=z_r=z^*}. \quad (11)$$

554 If individuals are indistinguishable when both types invest equally in cooperation ($z_h = z_r =$
555 z), then the viability functions satisfy $V_h(z, z) = V_r(z, z)$. In this case, Condition 11 can be
556 restated as

$$V_h^{z_h} + \frac{n_r}{n_h} V_r^{z_h} > V_r^{z_r} + \frac{n_h}{n_r} V_h^{z_h}. \quad (12)$$

557 This says that the contribution to total viability from the increased specialisation of helper indi-
558 viduals is strictly larger than the contribution to total viability from the increased specialisation
559 of reproductives. As a result, helpers are pre-disposed to become more helper-like as they can
560 gain larger viability gains for the group than the other type of individual.

561 Division of labour by an accelerating return from individual 562 specialisation

563 Division of labour by an accelerating return from individual specialisation can occur if either of
564 the third or fourth terms in the Taylor expansion (Equation 2) are positive in value ($W^{z_h z_h} > 0$
565 or $W^{z_r z_r} > 0$). Taking the second derivative of fitness (Equation 1) with respect to each trait
566 and evaluating at the critical point of uniform cooperation z^* , gives:

$$\left. \frac{\partial^2 W}{\partial z_h^2} \right|_{z_h=z_r=z^*} = 2n_h F' V_h^{z_h} + n_h F'' V_h + n_h F V_h^{z_h z_h} + n_r F V_r^{z_h z_h}, \quad (13)$$

$$\left. \frac{\partial^2 W}{\partial z_r^2} \right|_{z_h=z_r=z^*} = 2n_r F' V_r^{z_r} + n_r F'' V_r + n_h F V_h^{z_r z_r} + n_r F V_r^{z_r z_r}. \quad (14)$$

567 The terms of Equations 13 and 14 capture the second order effects of increased investment
 568 in cooperation. The first term of each captures the decline in the fitness benefit of increased
 569 cooperation due to the cross-interaction between fecundity and viability. For instance, as a
 570 helper invests more in cooperation (higher x), it increases its own viability (higher V_h), but its
 571 fecundity declines as well (lower F) and so the relative benefit of this increased viability is
 572 lessened (the cross term $F'V_h^{z_h}$ is negative). This represents a kind of decelerating return from
 573 cooperation. The second term of each captures the second-order effect of decreased investment
 574 in fecundity. If this term is positive, then this means that there is a diminishing fecundity cost
 575 to increased investment in cooperation, which can favour division of labour. The third and
 576 fourth terms capture the second order effect of increased investment in viability, that is: does
 577 each successive investment in the public good lead to a larger or smaller increase in viability
 578 than the previous investment of the same size? The return on investment (ROI) in viability is
 579 *accelerating* if $V_h^{z_h z_h} > 0$, $V_r^{z_h z_h} > 0$, $V_h^{z_r z_r} > 0$, and $V_r^{z_r z_r} > 0$. The ROI is diminishing if
 580 these second derivatives are negative: $V_h^{z_h z_h} < 0$, $V_r^{z_h z_h} < 0$, $V_h^{z_r z_r} < 0$, $V_r^{z_r z_r} < 0$.

581 Thus if either Equations 13 or 14 are positive, then division of labour is favoured to evolve.
 582 This gives the second condition for division of labour.

583 The accelerating returns from individual specialisation condition for division of labour

$$\begin{aligned} & \frac{n_h V_h^{z_h z_h} + n_r V_r^{z_h z_h}}{n_h V_h} \Big|_{z_h=z_r=z^*} + \frac{F''}{F} \Big|_{z_h=z_r=z^*} + 2 \frac{F'}{F} \frac{V_h^{z_h}}{V_h} \Big|_{z_h=z_r=z^*} > 0, \quad (15) \\ \text{or} \quad & \frac{n_h V_h^{z_r z_r} + n_r V_r^{z_r z_r}}{n_r V_r} \Big|_{z_h=z_r=z^*} + \frac{F''}{F} \Big|_{z_h=z_r=z^*} + 2 \frac{F'}{F} \frac{V_r^{z_r}}{V_r} \Big|_{z_h=z_r=z^*} > 0. \quad (16) \end{aligned}$$

584 Fixing our attention on just equation 15 (or equivalently on 16), this condition states that the
 585 sum of the second order viability effect from increased cooperation (first term on left hand side)
 586 and the second order fecundity effect of increased cooperation (second term on left hand side)
 587 must be larger than the marginal fecundity cost of increased investment in viability (third term
 588 on left hand side). Note that the third term on left hand side is always negative because in-
 589 creased investment in viability decreases the value of increased investment in fecundity. There-
 590 fore, division of labour by a single trait mutation can only happen if there is an accelerating
 591 ROI in at least one of: fecundity, $F(z)$; helper viability, $V_h(z_h, z_r)$; or reproductive viability,

$$V_r(z_h, z_r).$$

Division of labour by reciprocal specialisation

The last remaining scenario for division of labour is that the resident strategy of uniform cooperation is unstable to mutations in both traits, which can occur depending on the value of the last term of the Taylor expansion (Equation 2; $W^{z_h z_r} \Delta z_h \Delta z_r$). This kind of instability can arise if there is a joint mutation that affects the level of cooperation of both helpers and reproductives at the same time ($\Delta z_h \neq 0$ and $\Delta z_r \neq 0$). However, it could also occur if a slightly deleterious mutation in one trait invades by drift and destabilises the other trait so much that the population evolves away from the critical point. In either case, it will be found that same condition must be satisfied in order for division of labour to evolve. In the rest of this section, we give the general analysis of whether $(z_h, z_r) = (z^*, z^*)$ is unstable to two-trait mutations, and then consider a simplifying special case to clarify the biological interpretation of this analysis.

Suppose that the resident strategy of uniform cooperation $((z_h, z_r) = (z^*, z^*))$ is stable against single-trait mutations (i.e. conditions 15 and 16 not satisfied). Then the resident strategy is unstable to two-trait mutations if and only if the determinant of the Hessian is negative:

$$\frac{\partial^2 W}{\partial z_h^2} \frac{\partial^2 W}{\partial z_r^2} < \left(\frac{\partial^2 W}{\partial z_h \partial z_r} \right)^2. \quad (17)$$

This condition is satisfied if the strength of directional selection pushing the population back to the critical point along either of the trait-value directions is less than the strength of directional selection on a trait when moved off of the critical point along the other trait direction. To evaluate the Hessian condition, we first compute the second order cross derivatives:

$$\frac{\partial^2 W}{\partial z_h \partial z_r} \Big|_{z_h=z_r=z^*} = \frac{\partial^2 W}{\partial z_r \partial z_h} \Big|_{z_h=z_r=z^*} = F'(n_h V_h^{z_r} + n_r V_r^{z_h}) + F(n_h V_h^{yx} + n_r V_r^{yx}) \quad (18)$$

Here, we have used that $V_i^{z_h z_r} = V_i^{z_r z_h}$. Substituting this, and Equations 13 and 14, into the Hessian condition gives

The reciprocal specialisation condition for division of labour

$$n_h V_h n_r V_r \left(\frac{n_h V_h^{z_h z_h} + n_r V_r^{z_h z_h}}{n_h V_h} + \frac{F''}{F} + 2 \frac{F'}{F} \frac{V_h^{z_h}}{V_h} \right) \left(\frac{n_h V_h^{z_r z_r} + n_r V_r^{z_r z_r}}{n_r V_r} + \frac{F''}{F} + 2 \frac{F'}{F} \frac{V_r^{z_r}}{V_r} \right) \Big|_{z_h=z_r=z^*} < \left((n_h V_h^{y_x} + n_r V_r^{y_x}) + \frac{F'}{F} (n_h V_h^{z_r} + n_r V_r^{z_h}) \right)^2 \Big|_{z_h=z_r=z^*} \quad (19)$$

614 Assume that neither Condition 15, nor 16, is satisfied: i.e. the individual ROI is non-accelerating.
 615 Then the left-hand side of the inequality is strictly positive, which means that Condition 19
 616 is nontrivial. We will see in examples that Condition 19 can be satisfied, which means that
 617 division of labour can evolve by reciprocal specialisation even when the individual ROI is di-
 618 minishing.

619 To clarify further the biological meaning of Condition 19, consider a simple family of
 620 models in which viability and fecundity are linear functions. In this case, all second derivatives
 621 are zero, and so we get the simplified condition:

622 **Simplified reciprocal specialisation condition for division of labour**

$$4n_h V_h^{z_h} n_r V_r^{z_r} \Big|_{z_h=z_r=z^*} < \left((n_h V_h^{z_r} + n_r V_r^{z_h}) \right)^2 \Big|_{z_h=z_r=z^*} \quad (20)$$

623 In the case that the viability functions are *symmetric* (Equation 5), this condition further sim-
 624 plifies to

$$V_h^{z_h} \Big|_{z_h=z_r=z^*} < V_h^{z_r} \Big|_{z_h=z_r=z^*}. \quad (21)$$

625 This inequality is satisfied if the viability of reproductives increases faster with increased coop-
 626 eration from helpers, than it does from increased cooperation from reproductives. This makes
 627 clear that reciprocal specialisation can evolve if reproductives stand to gain more from help
 628 from helpers than they would gain by helping themselves.

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Competing Interests

The authors declare no competing interests.

Data Availability

The Matlab (R2020b) source code used to generate Figures 4D-F is available at <https://osf.io/nw8gz/>

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629 Appendix

630 A Group structure models

631 We now consider models that have specified spatial (or ‘network’) structures. We apply the
632 division of labour scenarios outlined in the Materials and Methods to study division of labour
633 in these graph models. We find simple, general conditions on the graph for when division of
634 labour can invade.

635 A.1 Division of labour by between-individual differences: stars and branch- 636 ing groups

637 Consider a star of n cells, with 1 focal cell, and $n - 1$ peripheral cells (Figure A1). Assume
638 that some function, $H(z)$, determines the amount of a shared resource produced by a cell with
639 level of cooperation z . And let $1 - \lambda$ be the proportion of benefits produced by an individual
640 that it keeps for itself, so that λ is the proportion of benefits that is shared equally by a cell’s
641 neighbours. If the peripheral cells in the star have phenotype z_h and the focal cell has phenotype
642 z_r , then

$$\begin{aligned} W(z_h, z_r) = (n - 1)F(z_h) \left((1 - \lambda)H(z_h) + \frac{\lambda}{n - 1}H(z_r) \right) \\ + F(z_r) ((1 - \lambda)H(z_r) + (n - 1)\lambda H(z_h)). \end{aligned} \quad (22)$$

643 The viability of a peripheral cell is $V_h(z_h, z_r) = (1 - \lambda)H(z_h) + \lambda H(z_r)/(n - 1)$, and the
644 viability of the focal cell is $V_r(z_h, z_r) = (1 - \lambda)H(z_r) + (n - 1)\lambda H(z_h)$. Equation 12 then
645 gives the following condition for division of labour by between-individual differences:

$$\frac{1}{1 - \frac{n-2}{n-1}\lambda} > \frac{1}{1 + (n - 2)\lambda}, \quad (23)$$

646 which holds for every positive $\lambda > 0$.

647 In a similar vein, consider a group with a branching structure, where alternating cells have

Figure A1: A star.

648 either a , or b neighbours, with $a < b$. We term the cells with a neighbours as edge cells and
 649 cells with b neighbours as node cells.¹ This gives the following expected fitness:

$$W(z_h, z_r) = n_h F(z_h) \left((1 - \lambda) H(z_h) + (a/b) \lambda H(z_r) \right) + n_r F(z_r) \left((1 - \lambda) H(z_r) + (b/a) \lambda H(z_h) \right), \quad (24)$$

650 where n_h is the number of edge cells and n_r is the number of node cells. Note that for any
 651 graph in which n_h cells have degree a , and n_r cells have degree b , we have that $n_h/n_r = b/a$.
 652 The viability of an edge cell is $V_h(z_h, z_r) = (1 - \lambda) H(z_h) + (a/b) \lambda H(z_r)$ and the viability of
 653 a node cell is $V_r(z_h, z_r) = (1 - \lambda) H(z_r) + (b/a) \lambda H(z_h)$. Equation 12 then gives the following
 654 condition for division of labour by between-individual differences:

$$\frac{1}{1 - \frac{b-a}{b} \lambda} > \frac{1}{1 + \frac{b-a}{a} \lambda}. \quad (25)$$

655 So, since $b > a$, we find that division of labour by between-individual differences occurs for all
 656 values of $\lambda > 0$ (any social trait).

657 A.2 General graph analysis: between-individual differences

658 Consider a graph with vertices $i = 1, 2, \dots, n$, each vertex with degree d_i . Let A_{ij} be the matrix
 659 of adjacencies: $A_{ij} = 0$ if there is no edge $i - j$, and for every edge $i - j$ we have $A_{ij} = -1/d_j$.

¹In order to avoid edge effects, we assume that the the group eventually wraps around on itself, creating the shape of a regular polyhedron: in the case of $a = 2$, $b = 3$, this would be the dodecahedron, with $n_h = 30$ edge cells and $n_r = 20$ node cells.

Moreover, $A_{ii} = 1$, for each i . Notice that the column sums of the matrix A are zero:

$$\sum_{i=1}^n A_{ij} = 0. \quad (26)$$

The fitness function of the group associated with this graph is

$$W = \sum_i F(z_i) \sum_j (\delta_{ij} + A_{ij}) H(z_j), \quad (27)$$

where z_i is the level of cooperation of the individual at vertex i , and $\delta_{ij} = 1$ if $i = j$ and 0 otherwise. The uniform cooperation strategy, $z_i = z \forall i$, has fitness

$$W = nF(z)H(z), \quad (28)$$

which is maximised for some $z = z^*$ between 0 and 1, by our assumption that F is decreasing in z and H is increasing in z .

We now restrict to the ‘marginal’ case that $F(z)$ and $H(z)$ are both linear functions. In this case we can, without loss of generality, take $F(z) = 1 - z$, and $H(z) = z$. The uniform cooperation strategy is given by $z^* = 1/2$. The first derivatives of W at the uniform strategy are given by:

$$\partial_i W|_{z^*} = -\frac{1}{2} \sum_j A_{ij}. \quad (29)$$

Notice that, for fixed i ,

$$\sum_j A_{ij} = 1 - \sum_{\text{edges } i-j} \frac{1}{d_j}. \quad (30)$$

If all the vertices of the graph have the *same degree*, $d_1 = d_2 = \dots = d$, then $\sum_j A_{ij} = 0$, and so the first derivatives all vanish. If one or more of the vertices, j , connected to i , does not have the degree d_i , then the sum, Equation 30, does not vanish. In this case, the uniform strategy is not stable, and division of labour can invade.

For example, consider the branching tree with 7 cells, shown in Figure A2. The A matrix

Figure A2: A tree.

676 of this tree is:

$$A = \begin{bmatrix} 1 & -1/3 & -1/3 & 0 & 0 & 0 & 0 \\ -1/2 & 1 & 0 & -1 & -1 & 0 & 0 \\ -1/2 & 0 & 1 & 0 & 0 & -1 & -1 \\ 0 & -1/3 & 0 & 1 & 0 & 0 & 0 \\ 0 & -1/3 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & -1/3 & 0 & 0 & 1 & 0 \\ 0 & 0 & -1/3 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (31)$$

677 Using Equation 29, it follows that

$$\partial_i W|_{q^*} = \begin{cases} +1/3 & i = 1 \\ +2/3 & i = 4, 5, 6, 7 \\ -5/2 & i = 2, 3 \end{cases} \quad (32)$$

678 So vertices 2 and 3 are ‘predisposed’ towards helping less, whereas the more peripheral ver-
679 tices ($i = 1, 4, 5, 6, 7$) are predisposed towards helping more. The vertices with the fewest
680 neighbours ($i = 4, 5, 6, 7$) are also the most predisposed towards helping more.

681 A.3 A ring of cells

682 Let us assume that the group is composed of n cells that form a one dimensional filament
683 wrapped into a ring, where n is an even number (Figure A3). Label the cells 1 through n , and
684 assume that 1 is neighbours with n . We assume that each cell in the filament shares social
685 benefits with only its direct neighbours. Suppose that ‘odd’ cells are putative helper cells, and

Figure A3: A ring of cells.

686 ‘even’ cells are reproductives. This gives the following fitness for the group:

$$W(z_h, z_r) = \frac{n}{2}F(z_h)\left((1-\lambda)H(z_h) + \lambda H(z_r)\right) + \frac{n}{2}F(z_r)\left((1-\lambda)H(z_r) + \lambda H(z_h)\right) \quad (33)$$

687 The viability of helpers is $V_h(z_h, z_r) = (1-\lambda)H(z_h) + \lambda H(z_r)$ and the viability of reproductives
 688 is $V_r(z_h, z_r) = (1-\lambda)H(z_r) + \lambda H(z_h)$. We now consider each of the possible routes by which
 689 division of labour can evolve.

690 Using equations 6 and 7, we find that $F'/F = -H'/H$ at the resident strategy of uniform
 691 cooperation for both helpers and reproductives and therefore that the condition for division of
 692 labour by between-individual differences (Equation 11) can never hold.

693 Assume that F is a linear function. If the returns from cooperation are non-increasing
 694 ($H'' \leq 0$), then we use condition 17 (Figure 5a), to find that division of labour is favoured if
 695 and only if

$$\lambda > \frac{1}{2} + \frac{-H''}{2(H')^2}. \quad (34)$$

696 In the case that $H'' = 0$, division of labour is favoured only if $\lambda > 1/2$. If H'' is less than
 697 zero, then the returns on investment are *decelerating*, and λ must be larger than $1/2$ in order
 698 for division of labour to be favoured.

699 A.4 A well-mixed group of cells

700 We now consider a group that is “well-mixed” such that cells share the benefits of cooperation
 701 with all other group members. That is, we let $1 - \lambda$ be the amount of benefits produced by an
 702 individual that it keeps for itself and λ is the amount of benefits that is shared equally by all

703 other cells in the group. This produces the following expected fitness function:

$$W(z_h, z_r) = n_h F(z_h) \left((1 - \lambda) H(z_h) + \lambda \frac{(n_h - 1) H(z_h) + n_r H(z_r)}{n - 1} \right) + n_r F(z_r) \left((1 - \lambda) H(z_r) + \lambda \frac{(n_r - 1) H(z_r) + n_h H(z_h)}{n - 1} \right), \quad (35)$$

704 where $n = n_h + n_r$ and we have that the viability of a helper is $V_h(z_h, z_r) = (1 - \lambda) H(z_h) +$
705 $\lambda \frac{(n_h - 1) H(z_h) + n_r H(z_r)}{n - 1}$ and the viability of a reproductive is $V_r(z_h, z_r) = (1 - \lambda) H(z_r) + \lambda \frac{(n_r - 1) H(z_r) + n_h H(z_h)}{n - 1}$.
706 Plugging these into equation 11 we find that division of labour cannot evolve by between-
707 individual differences as both sides are equal to H'/H , and thus helpers and reproductives face
708 the same viability-fecundity tradeoff.

709 If the returns from cooperation and fecundity are linear ($F'' = H'' = 0$), then we can
710 evaluate condition 20 directly to find that division of labour by reciprocal specialisation can
711 evolve if (Figure 5c)

$$\lambda > \frac{n - 1}{n}. \quad (36)$$

712 Otherwise, if the returns from cooperation are diminishing (say, $H'' < 0$, with F linear), then
713 we can use the general condition 17 to find,

$$\lambda > \frac{n - 1}{n} \frac{(1 + n_h x)(1 + n_r x)}{1 + \frac{n_h^2 + n_r^2}{n} x}, \quad \text{where } x = \frac{H'' F}{2 H' F'}. \quad (37)$$

714 Notice that, for diminishing returns ($H'' < 0$), we have that $x > 0$, and in this case it follows
715 that:

$$\frac{(1 + n_h x)(1 + n_r x)}{1 + \frac{n_h^2 + n_r^2}{n} x} > 1. \quad (38)$$

716 In other words, if $H'' < 0$, then λ must be *even higher* for division of labour to be favoured,
717 than when $H'' = 0$.

Figure A4: Some tessellation patterns, and the associated ranges of λ for which reciprocal specialisation is possible in each case. Each figure should be regarded as showing just a few cells of the infinite tessellation.

718 A.5 General graph analysis: reciprocal specialisation

719 We now return to the case of a general graph model, and consider when division of labour is
 720 possible via reciprocal specialisation. Once again, fix some graph G . Assume that the first
 721 derivatives, $\partial_i W$, vanish at the strategy of uniform cooperation ($z_i = z^*$). Recall (Equation 29)
 722 that this is equivalent to assuming that all the vertices of the graph G have the same degree, d .
 723 The matrix of second derivatives of W is

$$\text{Hess} = \frac{\partial^2 W}{\partial z_i \partial z_j} \bigg|_{q^*} = 2F'(z^*)H'(z^*) (\delta_{ij} - \lambda M_{ij}), \quad (39)$$

724 where M is a symmetrized version of the A matrix:

$$M_{ij} = \frac{1}{2}(A_{ij} + A_{ji}). \quad (40)$$

725 All vertices have the same degree, say d , so that the matrix M is given by

$$M_{ij} = \frac{1}{d}L_{ij}, \quad (41)$$

726 where L is the *Laplacian* matrix:

$$L_{ij} = \begin{cases} d & \text{if } i = j, \\ -1 & \text{if } i - j \text{ is an edge,} \\ 0 & \text{otherwise.} \end{cases} \quad (42)$$

727 The uniform strategy ($z = z^*$) is *unstable* if and only if the matrix Hess has one or more
728 positive eigenvalues. When $\lambda = 0$, Hess = $-2I$, where I is the identity. So all eigenvalues of
729 Hess for $\lambda = 0$ are negative, and the uniform strategy is stable. This agrees with the biological
730 intuition: when $\lambda = 0$, the group is not interacting socially, and so division of labour cannot
731 evolve. We would like to find λ^* (if it exists), such that division of labour is possible for $\lambda > \lambda^*$.
732 This corresponds to the smallest value of λ for which $\det(\text{Hess})$ vanishes. We can explicitly
733 evaluate the determinant as:

$$\det(\text{Hess})(\lambda) = \left(\frac{2\lambda}{d}\right)^n \mathcal{P}\left(\frac{d}{\lambda}\right), \quad (43)$$

734 where the *characteristic polynomial* $\mathcal{P}(x)$ is a degree n polynomial defined by:

$$\mathcal{P}(x) = \det(L - xI). \quad (44)$$

735 The roots of $\mathcal{P}(x)$ are all non-negative (this is because L is a symmetric matrix). Moreover,
736 $x = 0$ is a root of $\mathcal{P}(x)$. Let μ be the largest root of $\mathcal{P}(x)$; i.e. μ is the largest *eigenvalue* of
737 L . Then the smallest value of λ for which $\det(\text{Hess})(\lambda)$ vanishes is $\lambda^* = d/\mu$. It follows that
738 division of labour can evolve if and only if

$$\lambda\mu > d. \quad (45)$$

739 Recall that d is the number of neighbours that an individual cell has in the graph. The eigen-
740 value μ can be thought of (see below) as a measure of how ‘bipartitionable’ the graph is. The
741 inequality can then be interpreted loosely as follows: if the graph is made “more bipartite”, λ
742 can decrease. If the number of neighbours, d , is increased, λ must increase.

743 To further understand μ , a useful property of L is that, for any vector of numbers $x =$
 744 $(x_1, \dots, x_N)$:

$$x^T L x = \sum_{i,j=1}^n x_i L_{ij} x_j = \sum_{\substack{\text{edges} \\ i-j}} (x_i - x_j)^2. \quad (46)$$

745 The largest eigenvalue of L is

$$\mu = \max_x \frac{x^T L x}{x^T x}. \quad (47)$$

746 On the other hand,

$$\sum_{\substack{\text{edges} \\ i-j}} (x_i - x_j)^2 \leq \sum_{\substack{\text{edges} \\ i-j}} (x_i^2 + x_j^2) = 2d \sum_{i=1}^n x_i^2. \quad (48)$$

It follows that

$$\mu \leq 2d.$$

747 Moreover, if the graph is bipartite, choose any bipartite colouring of its vertices. Then, assign-
 748 ing $x = +1$ to vertices of one colour, and $x = -1$ to vertices of the other colour, we find
 749 that

$$\sum_{\substack{\text{edges} \\ i-j}} (x_i - x_j)^2 = \sum_{\text{edges}} 4 = 2dn. \quad (49)$$

750 This means that μ achieves its maximum value, $\mu = 2d$, for bipartite graphs. It can be shown
 751 that $\mu = 2d$ if and only if the graph is bipartite. μ can be regarded, therefore, as a measure
 752 of “how bipartite” a given graph is. Some representative examples for small ($N \leq 8$) graphs
 753 are given in Figures A5-A7. The rest of this section applies the above analysis to several basic
 754 families of examples.

Filaments of cells. A ring of n cells has degree $d = 2$, and the largest eigenvalue of the Laplacian matrix depends on whether N is even or odd:

$$\mu = \begin{cases} 4 & n \text{ even} \\ 2 - 2 \cos\left(\frac{(n-1)\pi}{n}\right) & n \text{ odd} \end{cases} \quad (50)$$

For n even, division of labour is possible if $\lambda > 1/2$. For large odd n , μ is approximately 4, and so division of labour is again possible for $\lambda > 1/2$. However, for small odd n , μ is less than 4. This means that, for small n , division of labour is “easier” for even numbers of cells than for odd numbers of cells. For some examples, see Figure A5.

Complete graphs. The complete graph with n cells has degree is $d = n - 1$ and the largest eigenvalue is²

$$\mu = n. \quad (51)$$

So reciprocal specialisation is possible only if $\lambda > (n - 1)/n$.

Tessellations. We can carry out similar computations for (infinitely extended) tessellation patterns. There are many bipartite tessellations, in both 2 and 3 dimensions. All of these have the maximum possible μ , i.e. $\mu = 2d$. Examples of this include the hexagonal lattice, the square lattice, and the 3d cube lattice: Figures A4(a),(b), and (c). Reciprocal specialisation is also possible in many tessellations which are not bipartite. An example with $d = 6$ is shown in Figure A4(c), which has $\mu = 8$. Finally, there are tessellations which are so far from being bipartite that reciprocal specialisation is not possible. An example with $d = 8$ is shown in Figure A4(d), which has $\mu = 8$. The condition $\lambda\mu > d$ cannot be satisfied with $\mu = d$, since λ is at most 1.

²In terms of Equation 47, a possible vector that achieves the maximum is $x_1 = +1$, $x_2 = -1$, and $x_3, x_4, \dots = 0$. For this vector, $x^T Lx = 4 + 2(N - 2) = 2N$ and $x^T x = 2$.

Figure A5: Values of μ for different filament ($d = 2$) graphs.

Figure A6: Values of μ for different trivalent ($d = 3$) graphs.

Figure A7: Values of μ for different $d = 4$ graphs.

B Random role allocation

We repeat the above analyses where we now assume that individuals adopt their phenotypes with a particular probability, independently of other individuals in the group. We find that, with random role allocation, division of labour is not possible (in the absence of accelerating individual returns on investment).

B.1 A ring of cells

Let p be the probability of adopting the role of a helper and investing x in cooperation and $1 - p$ as the probability of adopting the role of a reproductive and investing y in cooperation. In the case of a ring of cells, the number of helpers among a given cell's two neighbours is a binomial random variable, $k \in \{0, 1, 2\}$. This gives the expected fitness:

$$\begin{aligned} \langle W \rangle = & pF(z_h) \left((1 - \lambda)H(z_h) + \lambda \sum_{k=1}^2 \binom{2}{k} p^k (1 - p)^{2-k} (kH(z_h) + (2 - k)H(z_r)) \right) \\ & + (1 - p)F(z_r) \left((1 - \lambda)H(z_r) + \lambda \sum_{k=1}^2 \binom{2}{k} p^k (1 - p)^{2-k} (kH(z_h) + (2 - k)H(z_r)) \right). \end{aligned} \quad (52)$$

The first term is the expected fitness if the focal cell adopts the role of a helper and the second term is the expected fitness if the focal cell adopts the role of a reproductive. We can simplify the above fitness equation to:

$$\begin{aligned} \langle W \rangle(z_h, z_r) = & pF(z_h) \left((1 - \lambda)H(z_h) + \lambda(pH(z_h) + (1 - p)H(z_r)) \right) \\ & + (1 - p)F(z_r) \left((1 - \lambda)H(z_r) + \lambda(pH(z_h) + (1 - p)H(z_r)) \right), \end{aligned} \quad (53)$$

If we multiply the fitness equation by n^2 and approximate $n_h = pn$ and $n_r = (1 - p)n$, then we arrive at the final fitness equation:

$$\begin{aligned} \langle W \rangle(z_h, z_r) = & n_h F(z_h) \left((1 - \lambda)H(z_h)n + \lambda(n_h H(z_h) + n_r H(z_r)) \right) \\ & + n_r F(z_r) \left((1 - \lambda)H(z_r)n + \lambda(n_h H(z_h) + n_r H(z_r)) \right), \end{aligned} \quad (54)$$

where we now have that the expected viability of a helper is $V_h(z_h, z_r) = (1 - \lambda)H(z_h)n + \lambda(n_h H(z_h) + n_r H(z_r))$ and the expected viability of a reproductive is $V_r(z_h, z_r) = (1 - \lambda)H(z_r)n + \lambda(n_h H(z_h) + n_r H(z_r))$.

The function, Equation 54, can be analysed using the results of Section B. We find (as expected) that division of labour by between-individual differences is not possible for this function:

$$V_h^{z_h} + \frac{n_r}{n_h} V_r^{z_h} = nH(z^*) = V_r^{z_r} + \frac{n_h}{n_r} V_h^{z_h}. \quad (55)$$

Moreover, we can evaluate condition 20 directly to find that division of labour by reciprocal specialisation can only evolve if, (for linear functions F and H)

$$(n - \lambda n_r)(n - \lambda n_h) < n_h n_r \lambda^2. \quad (56)$$

It is impossible to satisfy this inequality for $\lambda \leq 1$. Thus, assuming linear or decelerating ROIs, we find that division of labour cannot evolve by reciprocal specialisation.

B.2 A branching group of cells

We approximate the fitness of the group as the expected fitness of a randomly chosen cell in the branching group. With probability n_h/n we choose an “edge cell” with a neighbours and with probability n_r/n , we choose a “node” cell with b neighbours (here $n_h + n_r = n$, $a < b$ and $n_h/n_r = b/a$). If the cell is an edge cell, the number of neighbouring cells that are helpers is a binomial random variable $k \in \{0, \dots, a\}$. If the cell is a node cell, the number of neighbouring cells that are helpers is a binomial random variable $k \in \{0, \dots, b\}$. Again, we let p be the probability that the cell adopts the role of a helper. Similar to the process above, we can derive a fitness equation of the form:

$$W(z_h, z_r) = n_h F(z_h) \left((1 - \lambda)H(z_h)n + \left(\frac{n_h}{n} \frac{a\lambda}{b} + \frac{n_r}{n} \frac{b\lambda}{a} \right) (n_h H(z_h) + n_r H(z_r)) \right) + n_r F(z_r) \left((1 - \lambda)H(z_r)n + \left(\frac{n_h}{n} \frac{a\lambda}{b} + \frac{n_r}{n} \frac{b\lambda}{a} \right) (n_h H(z_h) + n_r H(z_r)) \right), \quad (57)$$

where we have approximated $n_h = pn$ and $n_r = (1 - p)n$. We thus have that the viability of a helper is $V_h(z_h, z_r) = (1 - \lambda)H(z_h)n + \left(\frac{n_h}{n} \frac{a\lambda}{b} + \frac{n_r}{n} \frac{b\lambda}{a}\right)(n_h H(z_h) + n_r H(z_r))$ and the viability of a reproductive is $V_r(z_h, z_r) = (1 - \lambda)H(z_r)n + \left(\frac{n_h}{n} \frac{a\lambda}{b} + \frac{n_r}{n} \frac{b\lambda}{a}\right)(n_h H(z_h) + n_r H(z_r))$. For the particular case of $a = 2$ and $b = 3$ (a branching filament), we can use Equation 11 to show that division of labour by between-individual differences can never evolve.

Moreover, if the returns from cooperation and fecundity are linear ($F'' = H'' = 0$), then we can evaluate condition 20 directly to find that division of labour by reciprocal specialisation can only evolve if $\lambda > 1$, which is outside the physically permissible range of the parameter. Thus, division of labour can only evolve in this scenario if there are individual efficiency benefits from specialisation.

B.3 General graph analysis: Random allocation

In general, suppose that the assignment of phenotype is done randomly, according to a probability density function $\rho(z)$, such that $\int dz \rho(z) = 1$. Write $z_0 = \langle z \rangle$ for the average, and $\sigma^2 = \langle z^2 \rangle - \langle z \rangle^2$ for the variance of the distribution. The expected fitness, for an arbitrary graph model (Equation 27) is

$$\langle W \rangle = \sum_{i=1}^n \int dz_i \rho(z_i) F(z_i) H(z_i) - \lambda \sum_{j=1}^n \sum_{i \neq j} \int dz_i dz_j \rho(z_i) \rho(z_j) F(z_i) A_{ij} H(z_j). \quad (58)$$

Putting $F(z) = 1 - z$ and $H(z) = z$, this becomes

$$\langle W \rangle = n (z_0 - \sigma^2 - (1 - \lambda) z_0^2), \quad (59)$$

where we have used that

$$\sum_{j=1}^n \sum_{i \neq j} A_{ij} = - \sum_{j=1}^n A_{jj} = -n. \quad (60)$$

This calculation shows that the expected fitness of the group, $\langle W \rangle$, is independent of the group's graph structure. Moreover, notice that $\langle W \rangle$ is largest (for fixed z_0) if the distribution is chosen so that $\sigma^2 = 0$: i.e. the state of uniform cooperation. Division of labour would correspond to

827 $\sigma^2 > 0$. So *Division of labour cannot be favoured* (absent accelerating returns) if phenotypes
828 are assigned randomly.

829 To see this in greater detail, consider the distribution

$$\rho(q) = (1 - p)\delta(q - x) + p\delta(z - y). \quad (61)$$

830 Under this distribution, cells become a helper (phenotype z_h) with probability $1 - p$, and a
831 reproductive (phenotype z_r), with probability p . Then $z_0 = (1 - p)z_h + pz_r$, and

$$\sigma^2 = p(1 - p)(z_h - z_r)^2. \quad (62)$$

832 The total expected fitness is then

$$\frac{1}{n} \langle W \rangle = z_0 - p(1 - p)(z - z)^2 - (1 - \lambda)z_0^2. \quad (63)$$

833 If $\lambda \leq 1/2$, the function has a critical point at $z_h = z_r = z = 1/(2(1 - \lambda))$, where its first
834 derivatives vanish. We compute that the determinant of the Hessian of $\langle W \rangle$ at the critical point
835 is

$$4n^2(1 - \lambda)p(1 - p), \quad (64)$$

836 which is positive. So

$$z_h = z_r = z = \frac{1}{2(1 - \lambda)} \quad (65)$$

837 is a maximum of $\langle W \rangle$, for all choices of p , and $\lambda < 1/2$. If $\lambda \geq 1/2$, then $\langle W \rangle$ is maximised
838 for $z_h = z_r = z = 1$. In either case, division of labour is not favoured.

C Additional questions

C.1 Does division of labour by reciprocal specialisation produce an accelerating fitness benefit?

We consider a population of uniform cooperators with ESS level of cooperation z^* . We consider a mutation where both helpers and reproductives specialise in their respective functions such that $\Delta z_h = -\alpha \Delta z_r = \Delta z > 0$, where $\alpha > 0$ is the degree to which reproductives specialise more than helpers ($\alpha > 1$) or less than helpers ($\alpha < 1$). This gives the fitness of a mutant with reciprocal specialisation as:

$$W(z^* + \Delta z, z^* - \alpha \Delta z) \approx W(z^*, z^*) + \frac{1}{2}(W^{z_h z_h} + \alpha^2 W^{z_r z_r} - \alpha W^{z_h z_r}) \Delta z^2, \quad (66)$$

where we have assumed that there are no between individual differences and so $W^{z_h} = W^{z_r} = 0$ at the ESS strategy of uniform cooperation, z^* . What is the shape of the return from increased specialisation in this case? We solve for the second derivative of mutant fitness with respect to the degree of specialisation Δz :

$$\frac{\partial^2 W}{\partial \Delta z^2}(z^* + \Delta z, z^* - \alpha \Delta z) \approx \frac{1}{2}(W^{z_h z_h} + \alpha^2 W^{z_r z_r} - \alpha W^{z_h z_r}), \quad (67)$$

If this expression is positive, then the group fitness returns from reciprocal specialisation are accelerating. In contrast, if this expression is negative, then the group fitness returns from reciprocal specialisation are diminishing.

Let us now assume that the mutant has a higher fitness than the resident strategy of uniform cooperation, such that division of labour by reciprocal specialisation evolves ($W(z^* + \Delta z, z^* - \alpha \Delta z) > W(z^*, z^*)$). This means that the second term on the right hand side of Equation 66 is strictly positive, which occurs when $W^{z_h z_h} + \alpha^2 W^{z_r z_r} - \alpha W^{z_h z_r} > 0$. Importantly, this is the exact same condition as for an accelerating fitness return from reciprocal specialisation. Consequently, division of labour by reciprocal specialisation evolves if and only if the group fitness return from reciprocal specialisation is accelerating.

C.2 Does division of labour without accelerating returns from individual specialisation require that individuals have different viabilities?

In many cases, it makes more sense to consider the viability of the group as a whole rather than the viabilities of the individual cells in the group. For instance, in Volvocine algae, sterile flagella beaters provide a benefit to the group by keeping it afloat at the appropriate height in the water column for light absorption. In this instance, individuals literally sink or swim as a whole group and so all individuals have the same viability. Here we go through the general framework where we now assume that $V_h = V_r = V$.

Considering equation 11, we find that division of labour by between-individual differences occurs when:

$$\frac{V^{z_h}}{n_h} > \frac{V^{z_r}}{n_r} \quad (68)$$

this specifies that the average contribution by helpers to group viability by a small increase in cooperation is greater than the average contribution by reproductives to group viability by a small increase in cooperation. Thus, putative helpers are pre-disposed to cooperation.

Let us now assume that there are no between individual differences ($V^{z_h}/n_h = V^{z_r}/n_r$). Considering equations 15 and 16, we find that division of labour by an accelerating return from individual specialisation can arise if:

$$\frac{nV^{z_h z_h}}{n_h V} \Big|_{z_h=z_r=z^*} + \frac{F''}{F} \Big|_{z_h=z_r=z^*} + 2 \frac{F'}{F} \frac{V^{z_h}}{V} \Big|_{z_h=z_r=z^*} > 0 \text{ or} \quad (69)$$

$$\frac{nV^{z_r z_r}}{n_r V} \Big|_{z_h=z_r=z^*} + \frac{F''}{F} \Big|_{z_h=z_r=z^*} + 2 \frac{F'}{F} \frac{V^{z_r}}{V} \Big|_{z_h=z_r=z^*} > 0 \quad (70)$$

We thus find that division of labour can evolve if $V^{z_h z_h} > 0$, $V^{z_r z_r} > 0$ or $F'' > 0$. We now assume that there is a non-accelerating return from individual specialisation $V^{z_h z_h} = 0$, $V^{z_r z_r} = 0$ and $F'' = 0$. Considering equation 20, we find that the condition for division of labour by reciprocal specialisation is: $V^{z_h}/n_h > V^{z_r}/n_r$. However, this contradicts our assumption that there are no between-individual differences ($V^{z_h}/n_h = V^{z_r}/n_r$), and so reciprocal specialisa-

tion is not a pathway to division of labour. Consequently, if we assume that all individuals in the group have the same viability ($V_h = V_r = V$), then division of labour evolves by either: (1) between-individual differences; or (2) an accelerating return from individual specialisation.

In our main analysis, where different individuals may have different viabilities, the consequence to the fitness of the group when helpers have a lower viability is not modelled. Indeed, a helper produces the same amount of public good for the group regardless of its expected viability. This approximation is also made in the Yanni et al. (2020) models and in earlier models by Michod (2006). More realistically, helpers with a lower viability may be expected to produce a smaller total amount of public good over the course of the group life cycle. This in principle could limit the efficiency benefits of between-individual differences and of synergistic reciprocal specialisation. Capturing this feedback between cooperation and viability with a formal model would require additional assumptions, which we leave to future work.

C.3 What happens if the fitness costs and benefits of cooperation are additive?

In the main analysis, we have assumed that cooperation provides a viability benefit at a personal cost to fecundity, where individual fitness is the product of viability and fecundity. Here we assume instead that the benefits and costs of cooperation are additive, such that increased cooperation leads to an increase in group fecundity at a cost to personal fecundity. For ease of comparison we maintain the notation V_h and V_r , which now correspond to the fecundity benefit provided to helpers and reproductives by the cooperation of group members.

This gives the following fitness of the group:

$$W(z_h, z_r) = n_h \left(F(z_h) + V_h(z_h, z_r) \right) + n_r \left(F(z_r) + V_r(z_h, z_r) \right) \quad (71)$$

We can employ the Taylor expansion of fitness (Equation 2) to determine the three conditions leading to division of labour. First, we find that division of labour by between-individual dif-

905 ferences can arise if:

$$\frac{n_h V_h^{z_h} + n_r V_r^{z_h}}{n_h} > \frac{n_h V_h^{z_r} + n_r V_r^{z_r}}{n_r} \quad (72)$$

906 This shows that division of labour can evolve if some individuals (helpers) can provide larger
907 fecundity benefits for the group at the same fecundity cost as others (reproductives). Division
908 of labour by an accelerating return from individual specialisation can arise if:

$$\left(n_h F'' + n_h V_h^{z_h z_h} + n_r V_r^{z_h z_h} \right) \Big|_{z_h = z_r = z^*} > 0 \text{ or} \quad (73)$$

$$\left(n_r F'' + n_h V_h^{z_r z_r} + n_r V_r^{z_r z_r} \right) \Big|_{z_h = z_r = z^*} > 0 \quad (74)$$

909 This shows that division of labour by an accelerating return from individual specialisation can
910 arise if there is an accelerating return from decreased cooperation due to increased personal fe-
911 cundity $F'' > 0$, or an accelerating return from increased cooperation due to increased viability
912 of the group ($V_h^{z_h z_h}, V_r^{z_h z_h}, V_h^{z_r z_r}, V_r^{z_r z_r} > 0$). If none of the above hold, we find that reciprocal
913 specialisation can evolve if:

$$n_h V_h^{z_h z_r} + n_r V_r^{z_h z_r} < 0, \quad (75)$$

914 where we have assumed that $\Delta z_h = -\Delta z_r$. This states that there is interference between the
915 cooperative efforts of helpers and reproductives such that increased cooperation by helpers
916 leads to larger relative fecundity benefits for the group when reproductives cooperate less
917 ($V_h^{z_h z_r}, V_r^{z_h z_r} < 0$). There is an analogous effect when fitness is the product of fecundity
918 and viability (first term in small brackets on right-hand side of condition 17).

A)

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Linear or diminishing

Individual
returns

Uniform cooperation

B)

Accelerating

Individual
returns

Division of labour

A) No between-individual differences

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Uniform cooperation

B) With between-individual differences

Division of labour

A) Unilateral specialisation

Reproductive specialisation

Or

Helper specialisation

Diminishing group fitness benefits

Unilateral specialisation

Uniform cooperation

B) Reciprocal specialisation

Accelerating group fitness benefits

Reciprocal specialisation

Division of labour

A)

B)

C)

D)

E)

F)

A) Accelerating returns from individual specialisation

B) Between-individual differences

C) Reciprocal specialisation