

# Community lifespan, niche expansion and the evolution of interspecific cooperation

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## Abstract

Microbes live in dense and diverse communities where they deploy many traits that promote the growth and survival of neighbouring species, all the while also competing for shared resources. Because microbial communities are highly dynamic, the costs and benefits of species interactions change over the growth cycle of a community. How mutualistic interactions evolve under such demographic and ecological conditions is still poorly understood. Here, we develop an eco-evolutionary model to explore how different forms of helping with distinct fitness effects (rate-enhancing and yield-enhancing) affect the multiple phases of community growth, and its consequences for the evolution of mutualisms. We specifically focus on a form of yield-enhancing trait in which cooperation augments the common pool of resources, termed niche expansion. We show that although mutualisms in which cooperation increases partners growth rate are generally favoured at early stages of community growth, niche expansion can evolve at later stages where densities are high. Further, we find that niche expansion can promote the evolution of reproductive restraint, in which a focal species adaptively reduces its own growth rate to increase the density of partner species. Our findings suggest that yield-enhancing mutualisms are more prevalent in stable habitats with a constant supply of resources, and where populations typically live at high densities. In general, our findings highlight the need to integrate different components of population growth in the analysis of mutualisms to understand the composition and function of microbial communities.

## KEYWORDS

cross-feeding, demography, ecology, kin selection, mutualism, spatial structure

## 1 | INTRODUCTION

Microbial communities perform functions that are crucial to human health and to the survival of earth's ecosystems. They provide vital services to their hosts by breaking-down complex molecules into digestible foods and by protecting them against pathogens (Bess

et al., 2020; Buffie & Pamer, 2013), and they maintain ecosystems by cycling essential nutrients and removing toxic waste (Falkowski et al., 2008). To perform these functions, microbes produce a vast arsenal of secreted molecules such as nutrient-scavenging molecules (D'Onofrio et al., 2010), and digestive (Rakoff-Nahoum et al., 2016) and detoxifying enzymes (Yurtsev et al., 2016). Because

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heterospecific microbes can be in micro-scale proximity (Kim et al., 2020; Welch et al., 2016), secreted molecules can impact other community members rather than the producer alone (Adamowicz et al., 2018; Estrela et al., 2019; Frost et al., 2018; Kim et al., 2020; Stacy et al., 2014).

Behaviours that favour members of other species are a major evolutionary puzzle (Hamilton, 1964; Maynard Smith & Szathmáry, 1995; Trivers, 1971; West et al., 2007), for resources that an individual could use to promote its own growth and survival are instead redirected to benefit other members of the community. A wealth of theoretical models has sought to identify the conditions that promote the evolution of cooperation and prevent the spread of cheats through the population (Foster & Wenseleers, 2006; Frank, 1994; Leigh, 2010; Sachs et al., 2004). Some models suggest that when individuals form lifetime partnerships, cooperators are able to retaliate early against uncooperative partners, and therefore impose large fitness costs on cheating due to the long-lasting nature of interactions (Axelrod & Hamilton, 1981; Bull & Rice, 1991; Doebeli & Knowlton, 1998; Trivers, 1971). Other models suggest that cooperation can evolve even if interactions are transient, as long as cooperators can identify cheats before they provide any benefit (Bull & Rice, 1991; Noë & Hammerstein, 1994). Still, other models suggest that cooperation can evolve even after the onset of transient interactions if cooperators can impose sanctions on cheats (West et al., 2002).

These evolutionary models of mutualism consider static populations and assume that the fitness costs and benefits are independent of the ecological and demographic dynamics of populations. Microbial populations, however, are highly dynamic and the fitness of traits strongly depends on how they impact the different phases of the growth cycle. These growth phases include lag time, exponential growth rate, and yield at saturation, with each of these phases representing a component of fitness (Adkar et al., 2017; Li et al., 2018; Manhart et al., 2018; Manhart & Shakhnovich, 2018; Mori et al., 2019; Ram et al., 2019). The contribution of each of these components to overall fitness depends on a range of ecological and demographic factors (Lipson, 2015). For instance, in short-lived habitats, early growth has a stronger impact on fitness than other growth phases, and therefore, traits that shorten the lag phase tend to evolve even if they have a negative effect on later phases of the growth cycle (Adkar et al., 2017).

Accounting for this multidimensional nature of fitness is therefore crucial to understand the adaptive value of interspecific traits in microbial communities. Indeed, competitive and cooperative traits do not only affect the dynamics of the focal species but also the dynamics of partner species. Thus, to analyse the costs and benefits of interspecific traits, models need to track the impact of such traits on the dynamics of populations, their impact on the different growth phases and the contribution of each phase to fitness. Such dependency of fitness costs and benefits on the dynamics of populations has been highlighted in models of cooperative cross-feeding (Bull & Harcombe, 2009). These models show that interspecific aid that promotes the growth rate of partners can only drive the evolution of

mutualisms during a narrow range of the exponential growth phase and therefore do not lead to mutualisms during the lag phase, where densities are low, or during the stationary phase, where densities are high and resources become depleted.

This theoretical finding suggests that rate-enhancing mutualisms (e.g. detoxification mutualisms; Yurtsev et al., 2016) can only evolve when the growth phase is the main contributor to overall fitness. Empirical work, however, suggests that mutualisms can increase a partner's yield—rather than growth rate—by creating new resource pools. For instance, it has been shown that the production of extracellular enzymes in bacteria increases yield at a cost on rate (Ramin & Allison, 2019). In addition, maximization of growth is associated with well-mixed environments and transient communities, where cooperation is less likely to evolve. Maximization of yield, by contrast, is often associated with spatially structured environments, where cooperation is more likely to evolve (Bachmann et al., 2013; Nahum et al., 2011). Thus, the theoretical basis of mutualistic traits that affect different components of microbial fitness remains relatively obscure.

Here, we address this question by developing models for the evolution of mutualisms that incorporate different aspects of ecology, demography and genetic structuring. With a particular emphasis on cross-feeding interactions, we explore how community lifespan (time before dispersal to new environments) and traits that affect different fitness components interact to influence the evolution of mutualisms. We first focus on mutualisms that affect growth rates to establish a baseline scenario and then extend the model to include cases where interspecific partners expand the shared pool of local resources by increasing local carrying capacity. Finally, we explore how the tension between interspecific competition for shared limiting resources and different forms of mutualistic traits affects the evolution of mutualisms.

## 2 | MODEL AND METHODOLOGY

### 2.1 | Eco-evolutionary dynamics

We assume a metapopulation composed of a very large number of patches, in which each patch is colonized by an initial density  $d_0$  of individuals of the focal species *A*, and by an equal density  $d_0$  of individuals of the partner species *B*. Interactions between the two species influence their growth trajectories, which we model using standard logistic equations. The intrinsic growth rate of species *A* is  $\phi_A(z)$ , where  $z$  is the amount of help a focal individual of species *A* provides to individuals of species *B*. The intrinsic growth rate of the partner species *B* is  $\phi_B$ . Each individual of species *A* improves the growth rate of species *B* by a factor  $\beta(z)$ . Similarly, each individual of the partner species *B* improves the growth rate of the focal species *A* by a factor  $\alpha$ . There is density-dependent regulation in each patch, whose carrying capacity is  $K$ . The population of the focal species is composed of a resident strain that expresses a phenotype  $z$  and of a mutant strain that expresses the phenotype  $x = z + \delta$ , where  $\delta$  is

vanishingly small. Thus, the mutant strain deviates only slightly from the resident strain in its level of investment in helping. The growth trajectories of each species, including the resident and mutant strain of species A, are then given by

$$\dot{b} = \left( \phi_B + \frac{\beta(z)a + \beta(x)a_H}{b + \varepsilon} \right) \left( 1 - \frac{a + a_H + b}{K} \right) b, \quad (1)$$

$$\dot{a} = \left( \phi_A(z) + \frac{\alpha b}{a + a_H + \varepsilon} \right) \left( 1 - \frac{a + a_H + b}{K} \right) a, \quad (2)$$

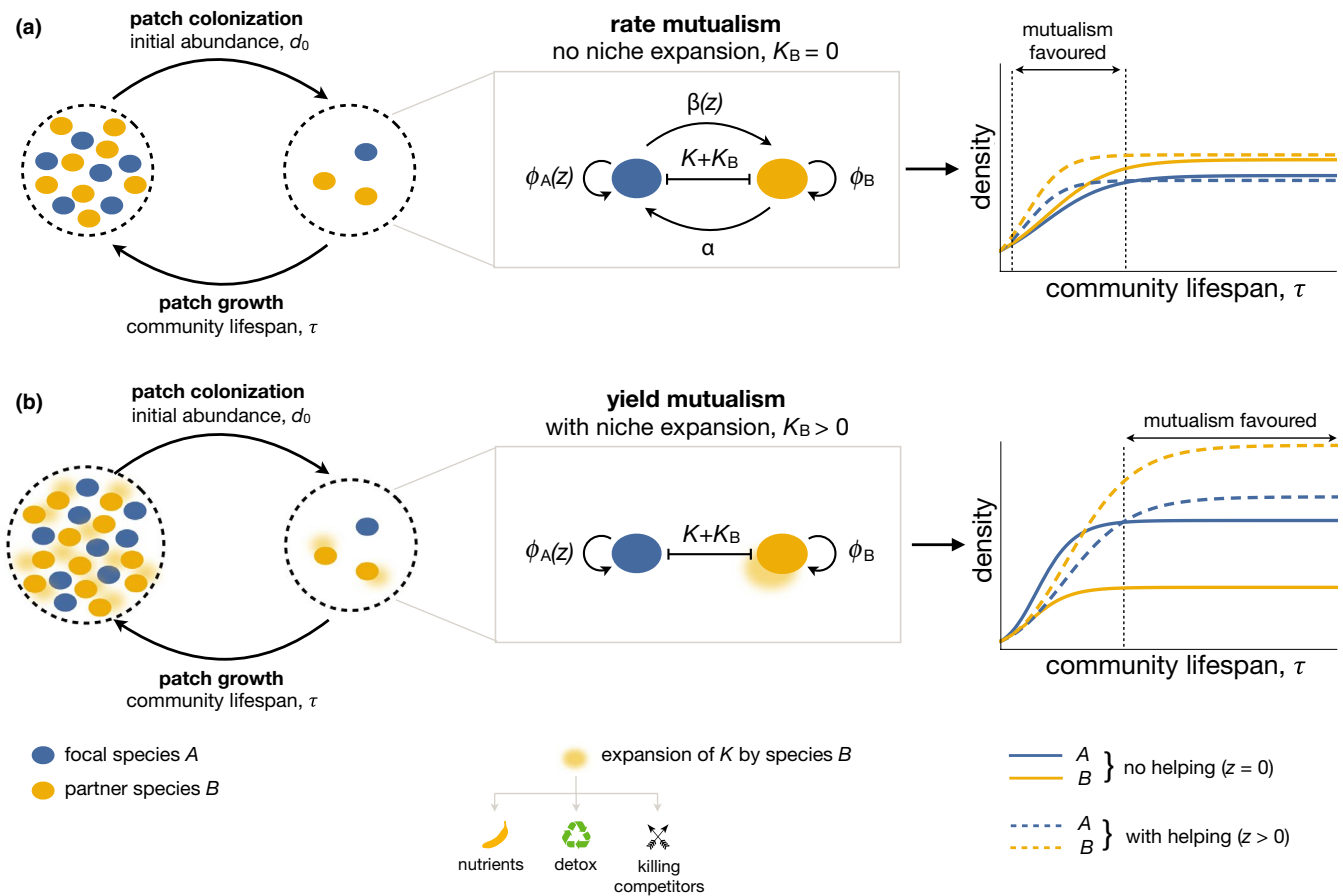
$$\dot{a}_H = \left( \phi_A(x) + \frac{\alpha b}{a + a_H + \varepsilon} \right) \left( 1 - \frac{a + a_H + b}{K} \right) a_H \quad (3)$$

where  $b$  is the density of the partner species B;  $a$  is the density of the resident strain of species A;  $a_H$  is the density of the mutant strain of species A; and  $\varepsilon$  is a constant that mediates the growth rates of each species. After the initial colonization of a focal patch, each species

grows during a period of time  $\tau$ , at which point there is competition for a new round of patch colonization events. Within each species, we assume that a proportion  $s$  of the competition occurs locally and a proportion  $1 - s$  occurs globally, where  $s$  is the scale of competition (Frank, 1998; Rodrigues & Gardner, 2013). Of the individuals competing to colonize each patch, only a density  $d_0$  of each species is successful. We assume that unsuccessful individuals die. After this, the life cycle of the community resumes (see Figure 1 for a schematic representation of the life cycle).

## 2.2 | Fitness and stable strategies

We focus on a helping trait that reduces the growth rate of species A and increases the growth rate of the partner species B. We assume that the growth rate  $\phi_A(z)$  of species A is a decreasing function of the investment in helping  $z$ , such that  $\phi_A(z) = \phi_{A,0} - \varphi_A z$  where  $\phi_{A,0}$  is the baseline growth rate of species A. Thus,  $d\phi_A(z)/$



**FIGURE 1** Model of the community lifecycle and interactions between species. We assume a metapopulation model where each patch is colonized by  $d_0$  individuals of the focal species A and of partner species B. Within each patch, species interact and grow until they disperse to a new empty patch. The carrying capacity of the patch is  $K$ . Two forms of mutualism are illustrated: (a) a case of rate mutualism where the focal species A pays a cost on its own intrinsic growth rate ( $\phi_A(z)$ ) to enhance the growth rate of its partner species B by a factor  $\beta(z)$ , and in return, species B improves the growth rate of species A by a factor  $\alpha$ . This is defined as a rate mutualism because interspecific cooperation causes the two species to grow faster at intermediate stages of community development (here  $K_B = 0$ ); (b) a case of yield mutualism in the form of reproductive restraint in the focal species A and niche expansion by B. Here, the focal species A grows more slowly, which promotes the growth of the partner species B, and consequently increases the carrying capacity of the local patch by  $K_B$  (here  $\alpha = \beta_0 = 0$ ). This is defined as a yield mutualism because interspecific cooperation causes both species to reach a higher equilibrium density

$dz < 0$ . In addition, we assume that the growth rate factor  $\beta(z)$  of species B is an increasing function of the helping effort  $z$  of species A, such that  $\beta(z) = \beta_0 z$  where  $\beta_0$  is the baseline growth rate of species B. Thus,  $d\beta(z)/dz > 0$  (see Figure S1 for a visual representation of the cost and benefit functions). Our aim is to understand how much helping  $z$  should individuals of the focal species A allocate to their partner species B. In other words, we want to determine the evolutionarily stable helping strategy  $z^*$ , which is the strategy that cannot be beaten by an alternative strategy  $z^* \pm \delta$  (Otto & Day, 2007). We assume that selection is weak, and the mutant allele is introduced in the population at a vanishingly small frequency (Otto & Day, 2007).

To determine the stable strategy  $z^*$  of a focal individual of our focal species A, we need to define the reproductive success of the different types of individuals in the population, which we define as the number of descendants an individual produces after one growth round following patch colonization. This is given by the final density of individuals in the local patch divided by the initial density of individuals in the same focal patch. Thus, in patches that include mutant individuals (i.e. cooperators), the reproductive success of a focal individual that expresses the resident strategy is  $f_R(x, z) = a(\tau)/(d_0(1-p))$ , whereas the reproductive success of a focal individual that expresses the alternative cooperative strategy is  $f_H(x, z) = a_H(\tau)/(d_0 p)$ , where  $p$  is the fraction of species A colonizers that are mutant individuals. In patches without mutant individuals (i.e.  $p = 0$ ), the reproductive success of a focal individual is given by  $f_G(z) = a(\tau)/d_0$ . A fraction  $s$  of the competition is local, in which case the focal individual competes with both clones of herself and wild-type individuals. The other fraction  $1 - s$  of the competition is global, in which case the focal individual competes with wild-type individuals only (Frank, 1998; Queller, 1994). Thus, the fitness of a focal individual expressing the alternative strategy  $x = z + \delta$  is given by

$$w(x, z) = \frac{f_H(x, z)}{s p f_H(x, z) + (1 - p) f_R(x, z) + (1 - s) f_G(z)}. \quad (4)$$

Note that the probability  $p$  is also the kin selection coefficient of relatedness  $r$  among individuals of species A within the focal patch (i.e.  $r = p$ ; Bulmer, 1994). Let  $g$  be the breeding value of the focal individual and  $g'$  be the breeding value of the focal individual's social partners, then the coefficient of relatedness is given by  $r = \text{cov}(g, g') / \text{cov}(g, g) = (p - p_0) / (p_C - p_0)$ , where  $p_0$  is the frequency of the allele in the population, and  $p_C$  is the probability that the cooperator carries the allele (Frank, 1998). Because the mutant allele is introduced in the metapopulation at a vanishingly small frequency,  $p_0 \approx 0$ , and because we are assuming haploid individuals,  $p_C = 1$ . Hence,  $r = p$ . That is, the coefficient of relatedness gives the probability that an intraspecific social partner within a patch carries an identical allele relative to the population average.

Because the alternative (mutant) helping strategy has a vanishingly small phenotypic effect, the selection gradient, denoted by  $S$ ,

is given by the slope of fitness on the phenotype (Otto & Day, 2007). Thus, we have

$$S(x, z) = \left. \frac{dw(x, z)}{dx} \right|_{x=z}. \quad (5)$$

An evolutionarily stable helping strategy  $z^*$  is found when the selection gradient is null. That is, when there is neither selection for slightly more investment in helping nor selection for slightly less investment in helping, and therefore  $S(z^*, z^*) = 0$  (Otto & Day, 2007). To find the evolutionarily stable strategy  $z^*$ , we implement an iterative numerical method (e.g. Otto & Day, 2007; Rodrigues, 2018). We solve the system of Equations (1–3) numerically to find the selection gradient  $S(x, z)$ . If the selection gradient is positive, the mutant allele invades and becomes the resident strategy. We repeat this procedure iteratively until we find the resident strategy  $z^*$  that cannot be invaded by a mutant allele.

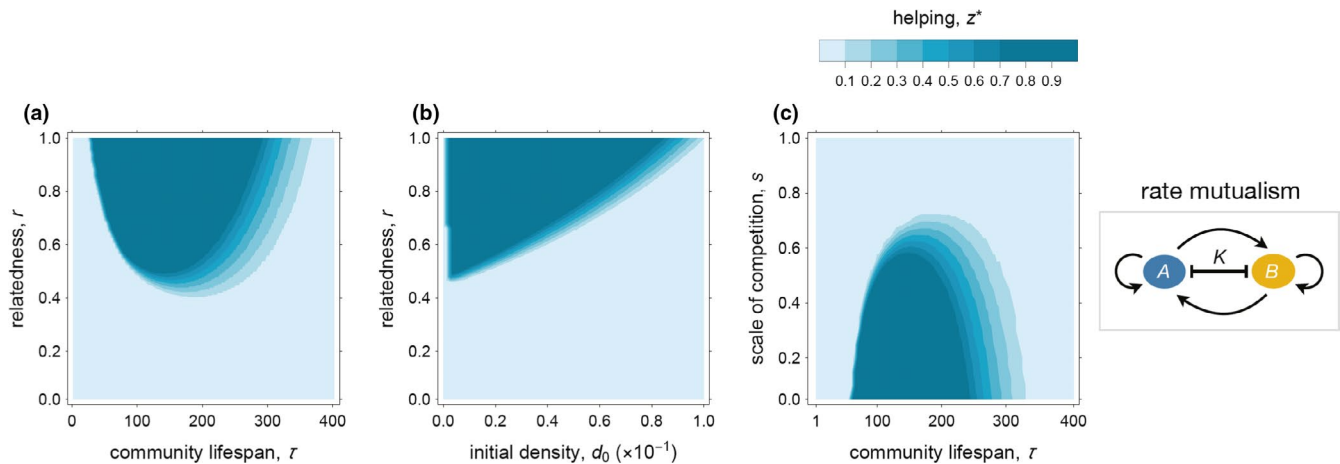
### 3 | RESULTS

#### 3.1 | Effect of genetic and demographic factors on the evolution of helping

Here, we study how the different genetic and demographic factors affect the optimal investment into helping behaviour.

##### 3.1.1 | Community lifespan

We start by investigating how community lifespan ( $\tau$ ) influences optimal investment in helping effort. We find that mutualism is favoured at intermediate values of the community lifespan and disfavoured when dispersal occurs at early or late stages of community development (Figure 2a). Note that early, intermediate and late community lifespan occur at low, intermediate and high community density, respectively (cf. Bull & Harcombe, 2009). When dispersal occurs during the early exponential phase of bacterial growth, cooperation is not favoured by selection because the costs of interspecific cooperation slow down the initial growth rate of cooperators. When dispersal occurs at later stages of community development (during the stationary phase), cooperation is also not favoured because interspecific competition is strong as resources are scarce and densities are high. This negative effect on cooperation at high densities arises because the carrying capacity is fixed, and therefore, as we approach the stationary phase the interaction between the two species becomes a zero-sum game. Any increase in the density of one species necessarily leads to a decrease in the density of the partner species. In contrast, at intermediate community lifespans, populations are still growing and interspecific cooperation is favoured because sufficient time has elapsed for cooperators to reap the benefits of their costly investment in helping and because interspecific competition



**FIGURE 2** Rate mutualisms are favoured at high levels of relatedness and when dispersal occurs at intermediate values of community lifespan. (a) The optimal investment in helping ( $z^*$ ) as a function of community lifespan ( $\tau$ ) and relatedness ( $r$ ). (b) The optimal investment in helping ( $z^*$ ) as a function of the initial density of bacteria ( $d_0$ ) and relatedness ( $r$ ). (c) The optimal investment in helping ( $z^*$ ) as a function of the intensity of local competition ( $s$ ) and community lifespan ( $\tau$ ). Parameter values:  $\phi_{A,0} = 0.012$ ,  $\phi_B = 0.011$ ,  $\alpha = 0.01$ ,  $\varepsilon = 10^{-4}$ ,  $K = 1$  and (a)  $s = 0.5$  and  $d_0 = 0.01$ , (b)  $\tau = 100$  and  $s = 0.5$ , (c)  $r = 0.5$  and  $d_0 = 0.01$

is still weak. However, competition with intraspecific cheats (low  $r$ ) can drastically reduce this ‘window of opportunity’ for interspecific cooperation, when relatedness falls below 0.5 (Figure 2a).

### 3.1.2 | Abundance of colonizers

We find that increasing the initial density of colonizers ( $d_0$ ) disfavors cooperation (Figure 2b) because it causes competition for local resources also to increase. As before, intraspecific cheats have a strong impact on the evolution of interspecific cooperation, which can rapidly drop from full helping (i.e.  $z^* = 1$ ) to no helping (i.e.  $z^* = 0$ ) when relatedness falls below 0.5.

### 3.1.3 | Scale of local competition

We find that as competition becomes more local (higher  $s$ ), competition among related individuals increases, and therefore, cooperation is less likely to evolve (Figure 2c). Moreover, under intense local competition, cooperation requires longer growth periods to evolve. Local competition, however, exerts less influence on optimal cooperative strategies when the dispersal stage occurs at higher densities (higher  $\tau$ ). This is because growth that occurs later in a community's lifespan is strongly regulated by the availability of local resources (i.e. density-dependent local regulation), and therefore, regulation of the population due to local competition becomes less important.

## 4 | MUTUALISM AND NICHE EXPANSION

So far, we have assumed a rate mutualism in which there is a growth rate cost for helpers and a growth rate benefit for recipients. This mirrors cases, for instance, of detoxification mutualisms in which

microbes protect each other by secreting enzymes that break down toxic compounds (e.g. beta-lactamases; Yurtsev et al., 2016). In many other cases, microbes secrete or excrete products that expand the resource pool by providing access to novel substrates (see Figure 1b). Such niche expansion captures the effect of traits like the release of metabolic waste by one species that opens a new niche for a cross-feeding species (incidental cross-feeding; Estrela et al., 2012; Goldford et al., 2018; Hillesland & Stahl, 2010; LaSarre et al., 2017); the secretion of exo-molecules that enhance nutrient supply like digestive enzymes and scavenging molecules (e.g. D'Onofrio et al., 2010; Flint et al., 2012; Rakoff-Nahoum et al., 2016); and the killing of competitors that opens up space for growth and access to new resources (Yanni et al., 2019). Here, we ask what is the role of niche expansion on the evolution of cooperation?

To address this question, we extend our base model to include a unidirectional cross-feeding relationship, impacting the yield of the community (see Figure 1b). The community carrying capacity becomes  $K = K_i + K_B$ , where  $K_i$  is the intrinsic carrying capacity and  $K_B$  is the component of the carrying capacity that depends on the density of the partner species B. This is given by

$$K_B = eK_i \frac{b}{k+b}, \quad (6)$$

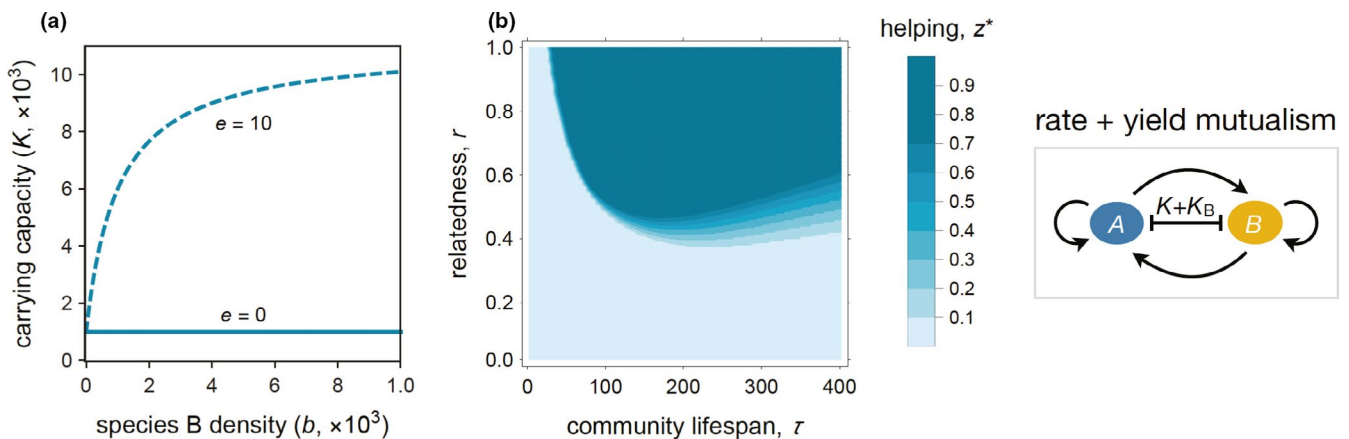
where  $e$  is a carrying capacity elasticity factor due to the presence of the partner species B, and  $k$  is a constant that determines how the carrying capacity increases with the density of the partner species (e.g. Frank, 2010). If we set elasticity to zero (i.e.  $e = 0$ ), we recover the base model, in which we have a rate mutualism with no niche expansion (i.e.  $K = K_i$ , see Figure 3a and Equations 1–3).

In the absence of elasticity (i.e.  $e = 0$ ), an increase in the density of the partner species inevitably results in increased competition for local resources between the focal cooperators and partner species, which precludes the evolution of cooperation at high densities, as described above. If the elasticity is sufficiently high, however, the

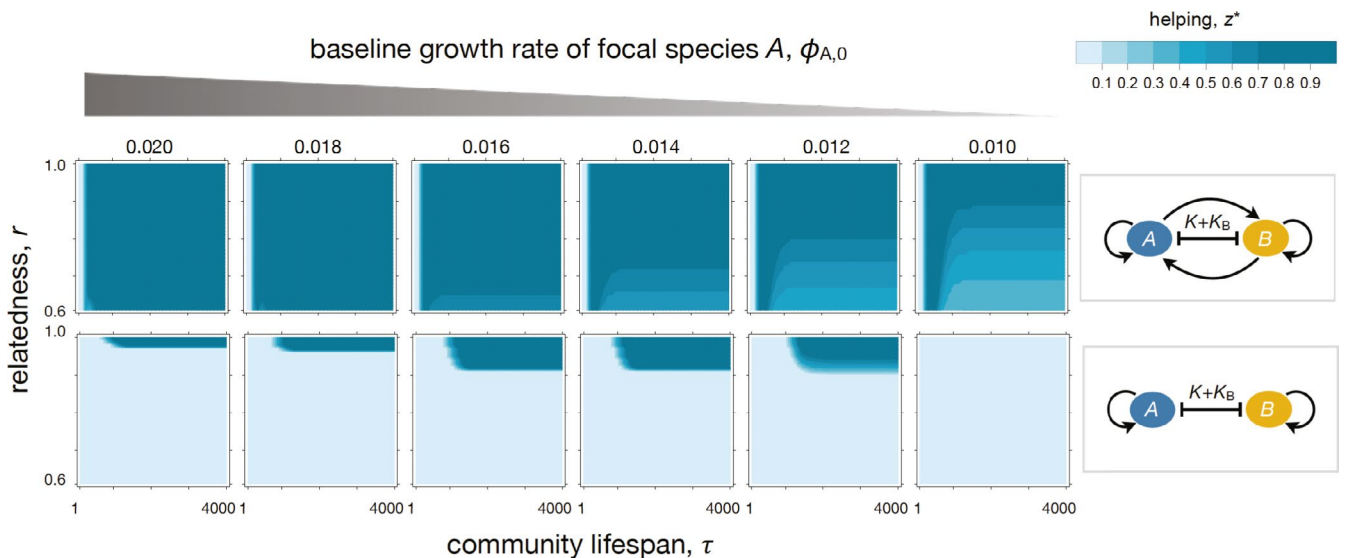
partner species provides additional resources that expand the carrying capacity of the local patch. As a result, an increase in the density of the partner species does not necessarily lead to increased competition for local resources. In fact, the additional resources provided by the partner species *B* can offset the additional competition for resources and favour cooperation at high densities, as shown in Figure 3b (see also Figure 4, top row).

So far, we have considered a scenario in which interspecific interactions influence the rate and the carrying capacity of each species simultaneously (i.e.  $\alpha > 0$ ,  $\beta_0 > 0$  and  $e > 0$ ). As a result, we cannot gauge which forces drive the evolution of the mutualism. To get around this, we now consider a simpler scenario in which

interspecific interactions do not affect the growth rate of both the focal and the partner species (i.e.  $\alpha = 0$ ,  $\beta_0 = 0$ ), but the partner species still promotes niche expansion via the production of additional resources ( $K_B$ ). We then ask under what conditions natural selection favours the evolution of cooperation in the focal species. As shown in Figure 4 (bottom row), although cooperation does not evolve at intermediate densities, it does evolve at high densities. Here, in contrast with the previous scenario, cooperation from the focal species *A* does not involve the secretion of any exo-products. Instead, cooperation takes the form of reproductive restraint in which individuals of the focal species *A* are selected to consume shared resources (replicate) more slowly (e.g. Kerr et al., 2006). By consuming shared



**FIGURE 3** Niche expansion facilitates the evolution of mutualism at high densities. (a) Carrying capacity as a function of the partner species *B* density for various levels of elasticity ( $e$ ). (b) Higher elasticity increases the window of opportunity in which cooperation is favoured by natural selection (see Figure 2a for the no elasticity baseline scenario) and may even favour cooperation at high densities. Parameter values:  $\phi_{A,0} = 0.012$ ,  $\phi_B = 0.011$ ,  $\epsilon = 10^{-4}$ ,  $s = 0.5$ ,  $k = 5$ ,  $\alpha = 0.01$ ,  $d_0 = 0.01$ ,  $e = 10$  and  $K_i = 1$



**FIGURE 4** Niche expansion favours the evolution of cooperation even in the absence of rate benefits. Optimal investment in helping ( $z^*$ ) as a function of community lifespan ( $\tau$ ) for various values of baseline growth rate ( $\phi_{A,0}$ ) and in the presence of niche expansion. When there are rate benefits (top row;  $\alpha = 0.01$ ,  $\beta_0 = 0.01$ ), mutualism evolves at intermediate and high densities. In the absence of rate benefits (bottom row;  $\alpha = 0$ ,  $\beta_0 = 0$ ), however, cooperation in the form of reproductive restraint evolves at high densities only and is highest at intermediate value of baseline growth rate. Parameter values:  $\phi_B = 0.011$ ,  $\epsilon = 10^{-4}$ ,  $s = 0.5$ ,  $k = 5$ ,  $d_0 = 0.01$ ,  $e = 10$  and  $K_i = 1$



resources more slowly, the partner species grows more rapidly and consequently produces more additional resources ( $K_B$ ). Thus, the cost of reproductive restraint is offset by the niche expansion that occurs later on in the community lifecycle due to the additional individuals of the partner species  $B$ . Restraint, however, only evolves when cheaters are rare (high relatedness).

The evolution of reproductive restraint depends on the relative growth rates of the two interacting species (Figures 4 and 5). This effect occurs because reproductive restraint has two contrasting effects on the fitness of the focal species. On the one hand, restraint reduces the fitness of the focal species because of the direct competition for limiting resources imposed by the partner species. On the other hand, restraint increases the fitness of the focal species because it increases the abundance of a partner species and this increases the carrying capacity of the local patch. As such, the smaller the baseline growth rate of the focal species relative to that of the partner species, the greater the fitness costs for the focal species at early stages of growth, which precludes the focal species to capitalize on the benefits of cooperation at later stages, and therefore, reproductive restraint does not evolve. In contrast, the greater the baseline growth rate of the focal species relative to that of the partner species, the more the fast-growing focal species suppresses the growth rate of the partner species, which reduces the benefits of cooperation that the focal species receives from the partner species at later stages of the community lifespan, and therefore, reproductive restraint is less favoured (Figure 4, bottom row). Our results are qualitatively similar if we consider an exponential or a power function for the niche expansion (Figures S2 and S3).

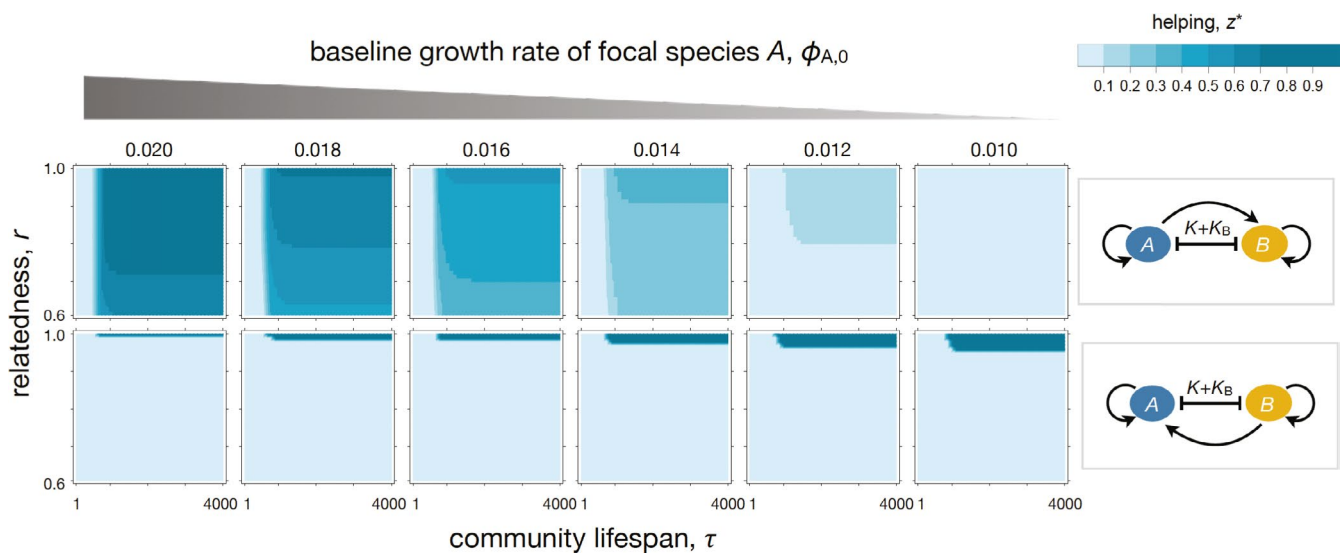
Next, we consider a scenario where the partner species expands the niche and the focal species increases the growth rate of the

partner species (i.e.  $\alpha = 0$ ,  $\beta_0 = 0.01$ ). Do we still observe the evolution of interspecific cooperation? We now find that cooperation is less likely to evolve (Figure 5). This happens because the benefits from niche expansion are not sufficient to offset the direct cost of cooperation arising from consuming common resources more slowly (restraint) and the indirect cost of cooperation that arise from the additional competition imposed by the increased growth of the partner species.

Finally, we consider a scenario in which the partner species expands the niche and also provides a growth rate benefit to the focal species (i.e.  $\alpha = 0.01$ ,  $\beta_0 = 0$ ). We find that the focal species evolves reproductive restraint when dispersal occurs at high densities, but not at intermediate or low densities (Figure 5). Here, restraint increases the density of the partner species, which in turn benefits the growth rate of the focal species, and also the yield when at high densities owing to niche expansion by the partner species. As shown above, such restraint behaviour only evolves when relatedness is very high.

## 5 | MUTUALISM AND NICHE OVERLAP

So far, we have assumed that both species,  $A$  and  $B$ , compete for the same resources (represented by the common carrying capacity  $K$ ). However, in many cases the niches of different species do not overlap or overlap only partially. We therefore extended the model to study the effect of niche overlap between the two species on the evolution of mutualism. The degree to which species  $A$  and  $B$  compete for resources—degree of niche overlap—is modelled by an interspecific competition coefficient, denoted by  $\gamma$ , which



**FIGURE 5** Evolution of restraint under different rate benefits. Optimal investment in helping ( $z^*$ ) as a function of community lifespan ( $\tau$ ) for various values of baseline growth rate ( $\phi_{A,0}$ ) and rate of benefits ( $\alpha$  or  $\beta_0$ ) in the presence of niche expansion. When only the partner species enjoys a rate benefit (top row;  $\alpha = 0$ ,  $\beta_0 = 0.01$ ), interspecies cooperation becomes unstable and only evolves when the baseline growth rate of the focal species  $A$  is sufficiently high. When there are rate benefits to species  $A$  only (bottom row;  $\alpha = 0.01$ ,  $\beta_0 = 0$ ), mutualism evolves when communities are long-lived and is favoured by lower baseline growth rate of the focal species. Parameter values:  $\phi_B = 0.011$ ,  $\varepsilon = 10^{-4}$ ,  $s = 0.5$ ,  $k = 5$ ,  $d_0 = 0.01$ ,  $e = 10$ , and  $K_i = 1$

varies from 1 (i.e. complete niche overlap) to 0 (i.e. nonoverlapping niches). This coefficient affects the density-dependent terms in Equations (1–3), such that they become:  $(1 - (\gamma(a + a_H) + b)/K)$  in Equation (1), which describes the growth trajectory of species *B*; and  $(1 - ((a + a_H) + \gamma b)/K)$ , in Equations (2) and (3), which describes the growth trajectories of species *A*. When there is complete niche overlap ( $\gamma = 1$ ), we recover our initial model. However, when niches do not overlap ( $\gamma = 0$ ), the density-dependent term of species *B* becomes  $1 - b/K$ , and the density-dependent term of species *A* becomes  $1 - (a + a_H)/K$ . This later scenario assumes that in the presence of niche expansion (i.e.  $K_B > 0$ ), the carrying capacities of species *A* and species *B* are equal yet their niches are fully segregated. Such yield-enhancing mutualism without niche overlap captures cases where species *B* produces two molecules, one that can only be consumed by species *A* and one that can only be consumed by species *B*.

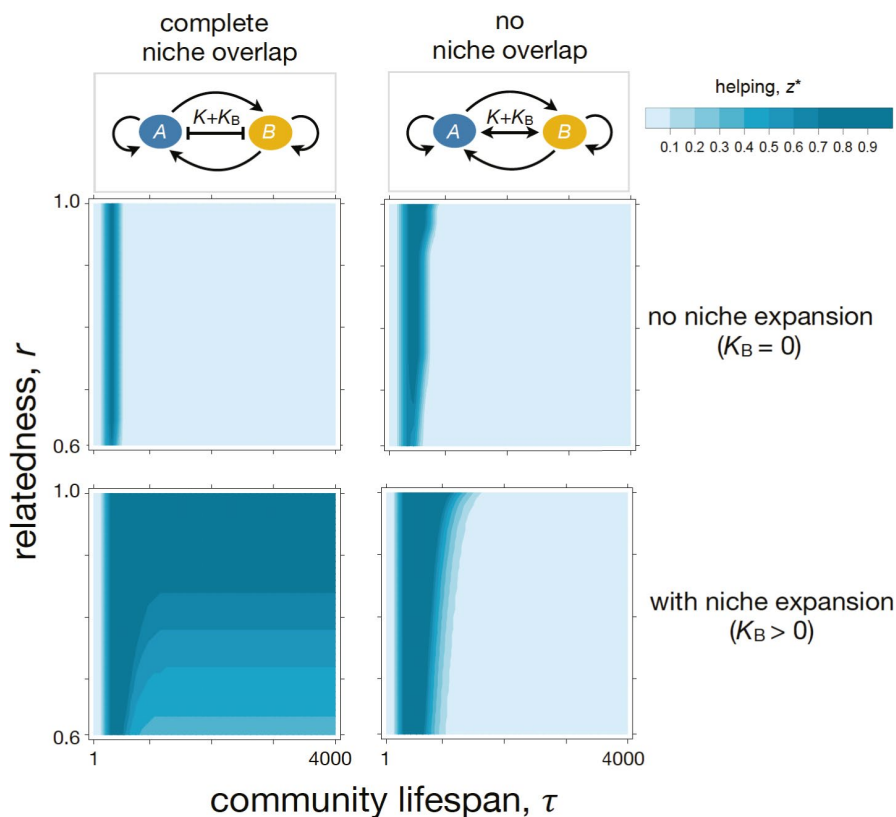
Given niche expansion by the partner species ( $K_B > 0$ ), relaxing competition for resources between the focal and partner species now reduces the strength of selection for reproductive restraint, making yield-enhancing mutualisms less likely to evolve (Figure 6 and Figure S4). Moreover, in such cases, mutualism with dispersal at later stages of community growth is no longer favoured when the degree of interspecific competition falls below 0.5 (Figure S4). The negative effect of lower interspecific competition on mutualism is especially pronounced in cases where the rate mutualism is turned-off (Figure S4, bottom row). Without niche expansion, cooperation at high densities is selected against regardless of the niche overlap (Figure 6). This result suggests that

interspecific cooperation in the form of reproductive restraint can only evolve when there is both a high degree of niche overlap and niche expansion.

## 6 | DISCUSSION

In mutualistic interactions, individuals receive a benefit from their interspecific partners. In such cases, individuals should care for the survival and growth of their interspecific partners to the extent that such care results in a higher probability of receiving a reciprocal benefit. In many cases, however, the niche overlap between species may lead to interspecific competition for shared limiting resources, which, in turn, may have an adverse impact on the evolution of mutualisms. Previous theory seeking to understand this problem in the context of microbial communities has shown that interspecific cooperation is more likely to evolve at intermediate densities (Bull & Harcombe, 2009). This outcome arises because at intermediate densities the benefits from interspecific cooperation are large enough to outweigh the initial costs of cooperation and because the intensity of density-dependent competition for resources is comparatively low.

The conclusion that mutualism evolves at intermediate densities relies on the assumption that individuals exchange resources that influence their growth rates. Mutualisms among microbes, however, are often yield-enhancing (Kolenbrander, 2011; Ramsey et al., 2011; Samuel & Gordon, 2006). Here we showed that in such cases interspecific cooperation can evolve even at high population densities



**FIGURE 6** Nonoverlapping niches disfavour the evolution of mutualism by reproductive restraint. Yield-enhancing mutualisms are sustained by reproductive restraint, which is only favoured under high degree of niche overlap. Rate-enhancing mutualisms, however, evolve regardless of the degree of niche overlap. Parameter values:  $\alpha = 0.01$ ,  $\beta_0 = 0.01$ ,  $\phi_{A,0} = 0.014$ ,  $\phi_B = 0.011$ ,  $\varepsilon = 10^{-4}$ ,  $s = 0.5$ ,  $k = 5$ ,  $d_0 = 0.01$ ,  $e = 10$  (in the presence of niche expansion), and  $K_i = 1$



**TABLE 1** Summary of the main conditions favouring the evolution of cooperation in the focal species for different forms of cooperation

Form of cooperation	Relatedness ( $r$ )	Community lifespan ( $\tau$ )	Niche overlap ( $\gamma$ )
Rate mutualism ( $\alpha > 0$ , $\beta_0 > 0$ , and $e = 0$ )	Intermediate to high	Intermediate	No/weak effect
Rate + yield mutualism ( $\alpha > 0$ , $\beta_0 > 0$ , and $e > 0$ )	Intermediate to high	Intermediate to high	No effect in short- and intermediate-lived communities; High in long-lived communities
Yield mutualism <sup>a</sup> ( $\alpha = 0$ , $\beta_0 = 0$ , and $e > 0$ )	Very high	High	High

<sup>a</sup>Cooperation in the focal species A takes the form of reproductive restraint.

(Table 1). In line with our findings, Rakoff-Nahoum et al. (2016) recently presented evidence of costly interspecific cooperation between Bacteroidales species that live at high densities in the human intestine. Specifically, *Bacteroides ovatus* secretes digestive enzymes that break down inulin, the products of which are then used by *Bacteroides vulgatus*, which, in turn, improves the fitness of *B. ovatus*. This study provides a rare example of a costly yield mutualism in a natural ecosystem. Evidence for costly mutualism between microbial species in a natural setting is still scarce, in part due to the difficulty of measuring the costs and benefits associated with a specific trait in complex environments such as the gut microbiota. Our study, however, suggests that rather than an exception, costly yield mutualisms may be a prevalent form of cooperative exchanges in the microbial world.

Understanding the nature of the costs and benefits accrued to individuals involved in interspecific exchanges is crucial for explaining the diversity and stability of mutualisms in microbial communities (e.g. Harcombe, 2010; Harcombe et al., 2018; Rakoff-Nahoum et al., 2016). In rate mutualisms, the benefits materialize more rapidly than in yield mutualisms, and so rate mutualisms are favoured at early stages of community growth (i.e. exponential phase of bacterial growth) whereas yield mutualisms are favoured at later growth stages (i.e. late-exponential and stationary phase). Given this difference in the rate of return of benefits, it is tempting to speculate that environmental conditions can predict the type of mutualism that is more likely to evolve in a given habitat. We hypothesize that natural selection favours rate mutualisms in more variable and transient environments in which individuals maximize the exploitation of the available nutritional niches and minimize nutritional losses (e.g. due to resource washout) and that in more stable and durable environments, natural selection should favour yield-enhancing mutualisms.

The evolution of interspecific cooperation also depends on the number of individuals that colonize a patch. If the density of colonizers is initially high, then there is intense competition for resources right from the start of community growth, which narrows the window of opportunity within which cooperation can evolve. Mixed genotypes in a patch, either due to mixed patch colonization or due to mutations, may also disrupt cooperation via two processes. Firstly, collective action at an early stage of the demographic dynamics is required to produce enough benefits at intermediate stages, which can only happen if there is a sufficiently high number of

cooperators during the early stages of community growth. Secondly, the benefits provided by the partner species at intermediate densities come in the form of public goods, and therefore all individuals of the focal species, both cooperators and cheats, benefit equally from the help provided by the partner species. As a result, high relatedness within the focal species ensures that the benefits of cooperation are directed towards cooperators, which prevents free-riders from exploiting the products of cooperation. Correlations between genotypes of partner species because of spatial structure may also affect the evolution of interspecific cooperation (Harcombe, 2010; Harcombe et al., 2018; Mitri et al., 2011), and evolutionary transitions from an autonomous to obligate cross-feeding species (Oliveira et al., 2014). Thus, exploring the relationship between within-species relatedness, assortment between partner species and population dynamics is an interesting area for future studies.

We also find that the evolution of cooperation in the form of reproductive restraint in the focal species depends on the relative intrinsic growth rate of the two partner species. Reproductive restraint can evolve if the intrinsic growth rate of the focal species is high enough so that its own growth is not suppressed by the growth of its partner species at early stages of community development, but not so high that the focal species suppresses the growth of its partner species, and consequently the benefits of cooperation accrued at later ages of the community lifespan. Broadly related to this idea, it has been shown that both growth rate differences between species and competition for a shared resource can affect the stability of cross-feeding interactions (Hammarlund et al., 2019). Starting with a bidirectional obligate cross-feeding mutualism between two species, Hammarlund et al. (2019) showed that when one partner becomes independent, coexistence can only be maintained when the obligate partner is the faster growing species but breaks down when the obligate partner is the slower grower. In our model, interspecific cooperation evolves between two species that can grow independently. It would be interesting to investigate whether restraint is more or less likely to evolve in systems where the partner species depends on the focal species for growth.

Our initial findings assumed that the focal and partner species compete for the same limiting resources, which is consistent with the idea of strong niche overlap. It has been suggested that low niche overlap and high relatedness can favour cooperation between species (Mitri & Foster, 2013). What happens if now the

focal and partner species compete less, or not at all, for the same resources—that is, if there is low or no niche overlap? Here, we find that interspecific cooperation, in the form of reproductive restraint, is favoured when interspecific competition is high but not when it is low. In other words, interspecific competition selects for interspecific cooperation. This effect occurs because without a shared limiting resource, the incentives for reproductive restraint are eliminated. Indeed, prudence in resource consumption no longer promotes the growth of the partner species and its associated yield-enhancing benefits, but it still carries the costs associated with intraspecific cheats. We would expect low niche overlap to favour other forms of interspecific cooperation that directly impact the yield of partner species.

We have assumed that cooperation is constitutively expressed. Under this scenario, rate mutualisms are favoured at intermediate densities whereas yield mutualisms are favoured at high densities. These contrasting selective pressures raise the hypothesis that natural selection favours the density-dependent regulation of these cooperative traits. It is now well understood that intraspecific microbial cooperation is commonly regulated in a density-dependent manner (Darch et al., 2012; Ghoul et al., 2016; Xavier et al., 2011), often controlled by cell–cell signalling mechanisms termed quorum sensing (Whiteley et al., 2017). Quorum sensing limits the expression of multiple social traits to high-density environments and limits the extent of intraspecific social cheating by positive-feedback control of cooperative behaviour (Allen et al., 2016). Although less studied, signalling between species has also been documented. The best studied interspecies quorum sensing molecule is the autoinducer AI2, which mediates interspecific communication and allows bacteria to determine their overall population density and regulate their behaviour accordingly (Xavier & Bassler, 2005). It is intriguing to consider the possibility that interspecific cooperation may also be regulated in a manner that depends on total community density. Specifically, we predict that rate-enhancing traits are more likely to be up-regulated during earlier growth phases (low densities) but down-regulated during later growth phases (high density). By contrast, we predict that yield-enhancing traits are down-regulated during earlier growth phases but up-regulated during later growth phases and the stationary phase.

We have adopted an open-model approach to social evolution, where relatedness and scale of competition are treated as independent model parameters (Foster & Wenseleers, 2006; Frank, 1998; Gardner & West, 2006). The advantage of this approach is that it allows for greater generality, as the association between relatedness and scale of competition is diverse (Brown & Taylor, 2010; Gardner & West, 2006; Kümmerli et al., 2009; Rodrigues & Taylor, 2018), and therefore, we can readily make predictions across a wide range of biological scenarios. For instance, the effect of limited dispersal on relatedness depends on the mode of dispersal, which can assume the form of individual, partial and complete budding (Rodrigues & Taylor, 2018). Under an individual mode of dispersal, limited dispersal increases both relatedness and local competition between relatives, which disfavours the evolution of intraspecific cooperation

(Kümmerli et al., 2009). In contrast, if individuals disperse in groups of relatives, that is partial or complete budding dispersal, high dispersal leads to high relatedness but low local competition, conditions that favour the evolution of intraspecific cooperation (Gardner & West, 2006; Kümmerli et al., 2009; Rodrigues & Taylor, 2018) and the evolution of interspecific cooperation as shown here. These examples illustrate that the natural history of each species drives specific associations between relatedness and the scale of competition, which will not only affect the evolution of intraspecific cooperation but also shape the evolution of interspecific cooperation. Exploring these different scenarios is an interesting area for future work.

In this paper, we have not considered co-evolution of the two species; we have assumed that the partner species remains in its ancestral form and expresses a constant level of helping. Helping in the partner species is, however, also a trait under the action of natural selection, and allowing for the co-evolution of helping between the two species may have important consequences for optimal levels of investment in cooperation (West et al., 2002). We have also assumed that the partner species is not able to discriminate between cooperators and cheats in the focal species (Allen et al., 2016). However, in the rhizobia-legume symbiosis, the plant can punish bacterial groups that do not help, and this mechanism has been shown to stabilize cooperation (West et al., 2002). Also, here we assume that the focal and partner species are both autonomous – the most likely starting point of mutualisms. The production of costly leaky goods or services can, however, select for the evolution of one-way metabolic dependencies to save on metabolic costs (Morris et al., 2012) and ultimately the evolution of interdependencies where microbes engage in the exchange of essential traits (Estrela et al., 2016). Extending our model in these multiple directions would be an interesting avenue for future studies.

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## PEER REVIEW

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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