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Private benefits and metabolic conflicts shape the emergence of microbial interdependencies

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Summary

Microbes perform many costly biological functions that benefit themselves, and may also benefit neighbouring cells. Losing the ability to perform such functions can be advantageous due to cost savings, but when they are essential for growth, organisms become dependent on ecological partners to compensate for those losses. When multiple functions may be lost, the ecological outcomes are potentially diverse, including independent organisms only; one-way dependency, where one partner performs all functions and others none; or mutual interdependency where partners perform complementary essential functions. What drives these different outcomes? We develop a model where organisms perform 'leaky' functions that provide both private and public benefits to explore the consequences of privatization level, costs and essentiality on influencing these outcomes. We show that mutual interdependency is favoured at intermediate levels of privatization for a broad range of conditions. One-way dependency, in contrast, is only favoured when privatization is low and loss-of-function benefits are accelerating. Our results suggest an interplay between privatization level and shape of benefits from loss in driving microbial dependencies. Given the ubiquity of microbial functions that are inevitably leaked and the ease of mutational inactivation, our findings may help to explain why microbial interdependencies are common in nature.

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Introduction

Microbes release a broad range of molecules into their environment both through the excretion of metabolic waste products (Lawrence *et al.*, 2012; Hom and Murray, 2014) and the secretion of functional exoproducts (Vetsigian *et al.*, 2011; Cordero *et al.*, 2012; Rakoff-Nahoum *et al.*, 2014). These metabolites modify their environment and set the stage for metabolic interactions with other microbes. The excretion of metabolic waste products can generate a broad range of ecological interactions; however, it is not a costly behaviour and therefore does not pose a challenge for evolutionary theory (Sachs *et al.*, 2004). This is in contrast with the costly secretion of functional exoproducts, as an individual that does not produce the metabolic function may have a selective advantage over producers (West *et al.*, 2006).

Compensated trait loss, which occurs when an individual has lost a trait whose function is compensated for by an ecological partner, is widespread in nature (Visser *et al.*, 2010; Ellers *et al.*, 2012). Of particular interest is the loss of functions that are essential for growth, as this leaves non-producers strictly dependent on other organisms in the community to perform these essential functions. The loss of essential functions can be driven by two key mechanisms, genetic drift and/or natural selection. For instance, some bacterial species living exclusively within host cells have evolved interdependencies through the reciprocal loss and retention of essential functions (Van Leuven *et al.*, 2014). Because these endosymbionts go through a tight bottleneck every host generation, their effective population size is relatively small and so neutral or even mildly deleterious mutations can accumulate by genetic drift, leading to the loss of essential functions (Kuo *et al.*, 2009; McCutcheon and Moran, 2012; Van Leuven *et al.*, 2014). But when microbes are free-living, the loss of essential functions is more likely to be driven by natural selection (Morris *et al.*, 2012; 2014; D'Souza *et al.*, 2014; Hillesland *et al.*, 2014).

The Black Queen (BQ) Hypothesis has been recently proposed to explain the adaptive loss of costly essential functions that are leaky, that is, functions that are unavoidably shared as they generate both private (retained by producer) and public (available to all members of the community) benefits (Morris *et al.*, 2012). Leaky functions are extremely common in nature (Morris, 2015), and when

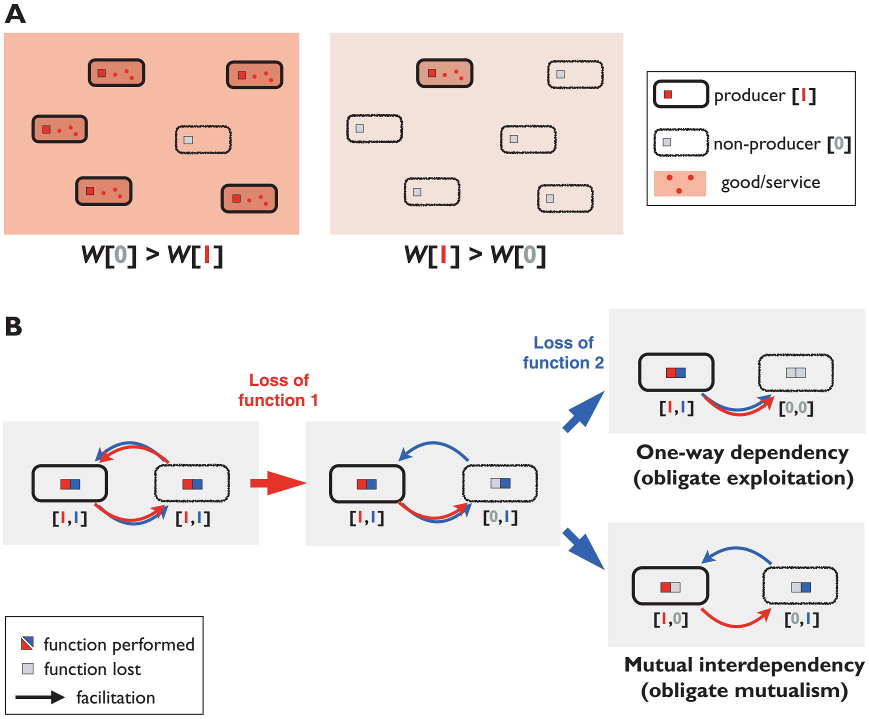

Fig. 1. A. Schematic illustrating the idea of negative-frequency dependence when a 'leaky' function is performed. Producers produce an intracellular good (e.g. catalase, red dot) that provides a service (e.g. detoxification; red shading). When producers are common, rare non-producers are favoured because they benefit from an environment where the service provided is abundant while saving on the costs of performing that function (left). When non-producers are common, the service provided is low, and consequently, producers are favoured because the private benefits compensate for the costs of performing the function (right). The darker the shading the greater the magnitude of the service provided (e.g. greater detoxification). *W* represents fitness.
B. Possible genotypes and some of the interactions emerging from loss of function when starting with a single genotype that performs two essential functions. A strain can either perform (1) or not perform (0) the function. Functions are represented by red and blue squares. Arrows show the function(s) performed by a given genotype. Genotypes are given by bit strings (see Model description section).

such functions are important components of fitness, it is common to find organisms that require the function, yet are unable to perform it themselves, in stable, long-term coexistence with organisms that perform the function. Dependencies centred around leaky functions are particularly evident in well-mixed and relatively stable ecosystems such as the microbial community of the open ocean, where highly abundant organisms such as the cyanobacterium *Prochlorococcus* and the heterotroph *Pelagibacter* depend on other community members for protection from hydrogen peroxide (Morris *et al.*, 2011), access to reduced sulfur compounds (Tripp *et al.*, 2008), and vitamins and other growth factors (Tripp *et al.*, 2009; D'Onofrio *et al.*, 2010; Giovannoni, 2012). The question then is what factors drive the adaptive loss of essential functions and consequent emergence of stable dependencies in well-mixed environments. The BQ Hypothesis posits that coexistence of producers and non-producers is stabilized by negative frequency dependence of fitness. The rationale is the following: when producers are common, rare non-producers are favoured because they benefit from an environment where the service provided by the function is abundant while saving on the costs of performing that function (Fig. 1A, left panel). But as the relative abundance of non-producers increases, the amount of service provided decreases, and therefore the growth advantage of non-producers decreases (Fig. 1A, right panel). The public benefit ultimately will be reduced to a level where the producers' private benefits compensate for the costs of performing the function, and therefore, both producers and non-producers have equivalent fitness. At that point, neither type can exclude the other as each type performs better than the other type when rare even in a well-mixed environment (Lenski and Hattingh, 1986; Morris *et al.*, 2014).

When different functions can be performed or lost, multiple ecological interactions along the conflict–mutualism continuum may arise. Previous theoretical and experimental work has provided valuable insight into understanding how costs (Frank, 1994a; Foster and Wenseleers, 2006; Bull and Harcombe, 2009; Wintermute and Silver, 2010; Mitri *et al.*, 2011; Pande *et al.*, 2014; Mee *et al.*, 2014; Oliveira *et al.*, 2014) and the degree of dependency (Estrela *et al.*, 2012; Estrela and Brown, 2013; Hom and

Murray, 2014; Müller *et al*., 2014; Oliveira *et al*., 2014) shape the dynamics and evolution of mutualisms. A limitation of these studies is that organisms can only exchange a single function, such as exchanging a resource for a resource (Wintermute and Silver, 2010; Pande *et al*., 2014; Hom and Murray, 2014; Mee *et al*., 2014; Müller *et al*., 2014) or a resource for a service (Estrela *et al*., 2012; Estrela and Brown, 2013). But in the event of multiple losses of essential functions, asymmetries in the number of functions that each genotype can perform may emerge. This raises the question of what conditions drive the evolution of one-way dependency such as obligate exploitation versus the evolution of mutual interdependency such as obligate mutualism (Fig. 1B). While this is beginning to get some attention theoretically (Oliveira *et al*., 2014), it remains poorly explored.

Also, little attention has been given to the role of partial privatization of metabolic functions in microbial interactions. A major reason for this is that the prevalence of partial privatization in microbes has been underestimated. Traditionally, most costly diffusible products were seen as fully public goods, that is, equally available to all cells sharing an environment. However, growing evidence suggests that microbial cells retain a fraction of the products of some metabolic functions, with the remaining fraction either actively secreted or else inevitably leaked into the environment, resulting in a partitioning of the function's benefits into private and public components. Examples of partially privatized traits in microbes are diverse and include the production of detoxifying enzymes (e.g., catalase; Morris *et al*., 2014), enzymes that degrade antibiotics (e.g. beta-lactamase; Livermore, 1995; Yurtsev *et al*., 2013), nutrient-scavenging molecules (e.g., siderophores; Scholz and Greenberg, 2015), enzymes that break down complex polysaccharides into simple nutrients (e.g. invertase; Gore *et al*., 2009) and molecules that act as biosurfactants (e.g. putisolvin; Cárcamo-Oyarce *et al*., 2015).

Despite the rising awareness that some microbial traits are partially privatized and that privatization has important consequences for the evolution of cooperation (Morris *et al*., 2012; Sachs and Hollowell, 2012; Strassmann and Queller, 2014; Morris, 2015), few models have investigated the consequences of partial privatization for microbial interactions. Here we extend a standard ecological model of species interactions to investigate the consequences of partial privatization of leaky functions for microbial dependencies. Focusing on a community where two functions may be lost, we find that high levels of privatization favour independent (autonomous) genotypes, whereas low levels of privatization tend to favour some level of exploitation. Interestingly, intermediate levels of privatization favour mutual interdependency, whereas one-way dependency is only favoured when privatization is low and the benefits from loss of function are accelerating. We then further extend our model to consider explicit spatial structure. Our spatial model reveals conditions that may allow mutual interdependency to dominate without exploitation from a genotype performing no functions by finding refuge at the moving front of a spatially expanding community.

Results

Model description

Our model tracks the dynamics of strains that perform BQ functions: i.e., those that are essential, costly and leaky. 'Leaky' means that the function is partitioned between a purely private and an unavoidably shared (leaked) public component. Consider a community with S strains and n functions. A strain can either perform or not perform the function, and the state of function j in strain i is denoted $a_{i,j}$ (with $a_{i,j} \in \{0,1\}$) (see Table 1 for a full list of the parameters used in the model). Performing a function is a consequence of producing a good or a service, and so we call a type that performs a function a producer. A producer strain incurs an individual cost that reduces its growth rate (g_i) so that:

$$g_i = g_{max} - c\left(\frac{\sum_{j=1}^{n} a_{i,j}}{n}\right)^{\theta} \tag{1}$$

Table 1. Summary of model parameters.

Symbol	Description	Equation
S	Number of strains in the community	(2), (3)
n	Total number of functions performed by the community	(1), (2)
$a_{i,j}$	Production state of the *j*th function by the *i*th strain	(1)
g_{max}	Maximum growth rate	(1)
c	Individual cost of production when performing all n functions	(1)
θ	Shape of the cost function	(1)
N	Population density	(2), (3)
z	Fraction of benefit from production that remains private	(2)
γ	Public/private effectiveness factor	(2)
d_{min}	Minimum death rate	(2)
d_{max}	Maximum death rate (a measure of essentiality)	(2)
$\varkappa$	Carrying capacity supported by the environment when the death term is zero	(3)

where g_{max} represents the growth of a genotype that does not perform any function (i.e. a non-producer, in which $a_{i,j} = 0$ for all j) and c is the total cost paid by a genotype that performs all n functions. To ensure that g_i remains positive, we restrict our analysis to cases where $g_{max} > c$. The term θ defines the shape of the cost function, such that when $\theta = 1$, costs increase linearly with increasing number of functions performed; when $\theta < 1$, costs decelerate with increasing number of functions performed (i.e. accelerating benefits from loss of function); and when $\theta > 1$, costs accelerate with increasing number of functions performed (i.e. diminishing benefits from loss of function) (Fig. S1A).

A producer strain gains a private benefit from production defined by a reduced death rate. Biologically, this can be seen as detoxification (e.g. Morris *et al.*, 2014) or antibiotic degradation (e.g. Yurtsev *et al.*, 2013). Although we focus here on functions that reduce death, growth-promoting functions are also potential candidates for BQ interactions (e.g. through the provision of essential nutrients; Gore *et al.*, 2009). In addition, both producers and non-producers receive a public benefit from production that depends on the density (N) of producers and the number of functions performed by each strain. The death term (d_i) is thus defined by:

$$d_i = (d_{\max} - d_{\min})\, exp\left[-\prod_{j=1}^{n}\left(a_{i,j}\,\underbrace{z}_{\substack{private\\benefit}} + \underbrace{\gamma(1-z)}_{\substack{public\\benefit}}\sum_{k=1}^{S} a_{k,j}N_k\right)\right] + d_{\min} \tag{2}$$

where z is the fraction of the benefit from production that remains private and $1 - z$ is the fraction of the benefit from production that is available to all members of the community composed of S strains (and which can be viewed as the 'leakiness' of the function; Morris *et al.*, 2012). We assume $0 \le z \le 1$, so when $z = 0$ the benefits from production are fully public, whereas when $z = 1$ the benefits from production are fully private. The term γ is a measure of public/private effectiveness, so when γ is high detoxification is more effective extracellularly than intracellularly, whereas when γ is relatively low, detoxification is more effective intracellularly than extracellularly. Note that we assume that the public good component is both non-excludable and non-rivalrous, that is, all individuals present in the environment have equal access to the good and one individual's use does not reduce its availability to other individuals (Dionisio and Gordo, 2006), a scenario that is more likely to happen for interactions involving detoxification. Furthermore, a strain dies at a minimum rate d_{min}, thus ensuring that the population suffers some death even when the public and private benefits are high (i.e., the environment is fully detoxified). Thus, as the number of functions performed increases and/or the number of producers increases, the death rate (d_i) decreases, generally exponentially with a lower limit at d_{min} (Fig. S1B). The degree of essentiality is captured by d_{max} such that as d_{max} increases, essentiality increases. Finally, assuming that population growth follows the logistic equation, the dynamics of the i^{th} strain in a community with S strains is given by:

$$\frac{dN_i}{dt} = \left[g_i\left(1 - \frac{\sum_{k=1}^{S} N_k}{\varkappa}\right) - d_i\right]N_i \tag{3}$$

where $\varkappa$ is the carrying capacity supported by the environment when the death term (d_i) is zero. Any function becomes 'strictly essential' if $d_{max} = g_{max}$. To understand this condition, we note that $g_i \le g_{max}$ (Eq. 1) and $d_i = d_{max}$ if any of the biological functions is not performed by the community (Eq. 2). Thus, if $d_{max} = g_{max}$ then $dN_i/dt < 0$. (Eq. 3). Without any one of the functions, the condition $d_{max} = g_{max}$, is sufficient to ensure extinction (i.e. function is strictly essential), and therefore non-producing individuals can only grow in the presence of producers. The coefficients for intra- and interspecific competitions are unity, thus, any benefits from interspecific association will be due to a reduction in death rate through BQ interactions. In the limit where d_i tends to 0, the model becomes identical to the classic competitive Lotka–Volterra equations (Otto and Day, 2007).

Our goal here is to investigate what factors favour mutual interdependency (obligate mutualism) versus one-way dependency (obligate exploitation). In particular, we are interested in understanding how varying some of the key factors driving BQ interactions, namely (i) privatization level (i.e. the level of private benefits relative to public benefits), (ii) the cost incurred from performing a function and (iii) the essentiality of the function, combine to affect the dynamics and outcome of loss-of-function interactions. Here we focus on the simplest scenario where obligate mutualism and obligate exploitation can potentially occur. This happens when a strain performs two functions ($n = 2$). Under these conditions, the double producer [1,1] can lose either or both of these functions. The strains that may arise are: single producers (either performing the first function only [1,0] or the second function only [0,1]), and a non-producer [0,0] (Fig. 1B). With this, the outcomes of competition are potentially diverse: double producer alone [1,1], obligate mutualism ([1,0] + [0,1]) where strains are interdependent and benefit mutually from association (Bronstein, 1994), pure obligate exploitation ([1,1] + [0,0]) where one strain depends on and benefits at the expense of another strain, and other exploitative outcomes (([1,1] + [1,0] + [0,1]), ([1,0] + [0,1] + [0,0]), and ([1,1] + [1,0] + [0,1] + [0,0])).

Mutualistic exchange of complementary functions is favoured by partial privatization

We start by investigating the effect of varying the level of privatization (z) and cost (c) on the density of the double producer when grown alone. We find that higher costs lead to lower densities, as expected (Fig. S2A). The effect of privatization, however, depends on the value of the public/private effectiveness factor (γ). Although double producers benefit from greater privatization if γ is low, they benefit from lower privatization if γ is high (Fig. S2A). Biologically, this negative effect of high privatization when γ is high can be viewed as a detrimental effect of having the toxic substance entering into the cell, such that an individual cell is generally better off if detoxification occurs extracellularly rather than intracellularly. It should be noted, however, that under these conditions, higher privatization can rescue the population from extinction when producers are rare (Fig. S2B). We focus on this high-γ scenario in the following analyses.

We next examine what happens when the double producer interacts with loss-of-function genotypes, including the two complementary single producers and the non-producer. We find that diverse outcomes are possible, including full extinction, various types of coexistence spanning the conflict–mutualism continuum, and single strain (double producer alone, or, when the functions are not strictly essential, non-producer alone) (Fig. 2). In particular, the two single producers are favoured by intermediate levels of privatization for a broad range of costs and

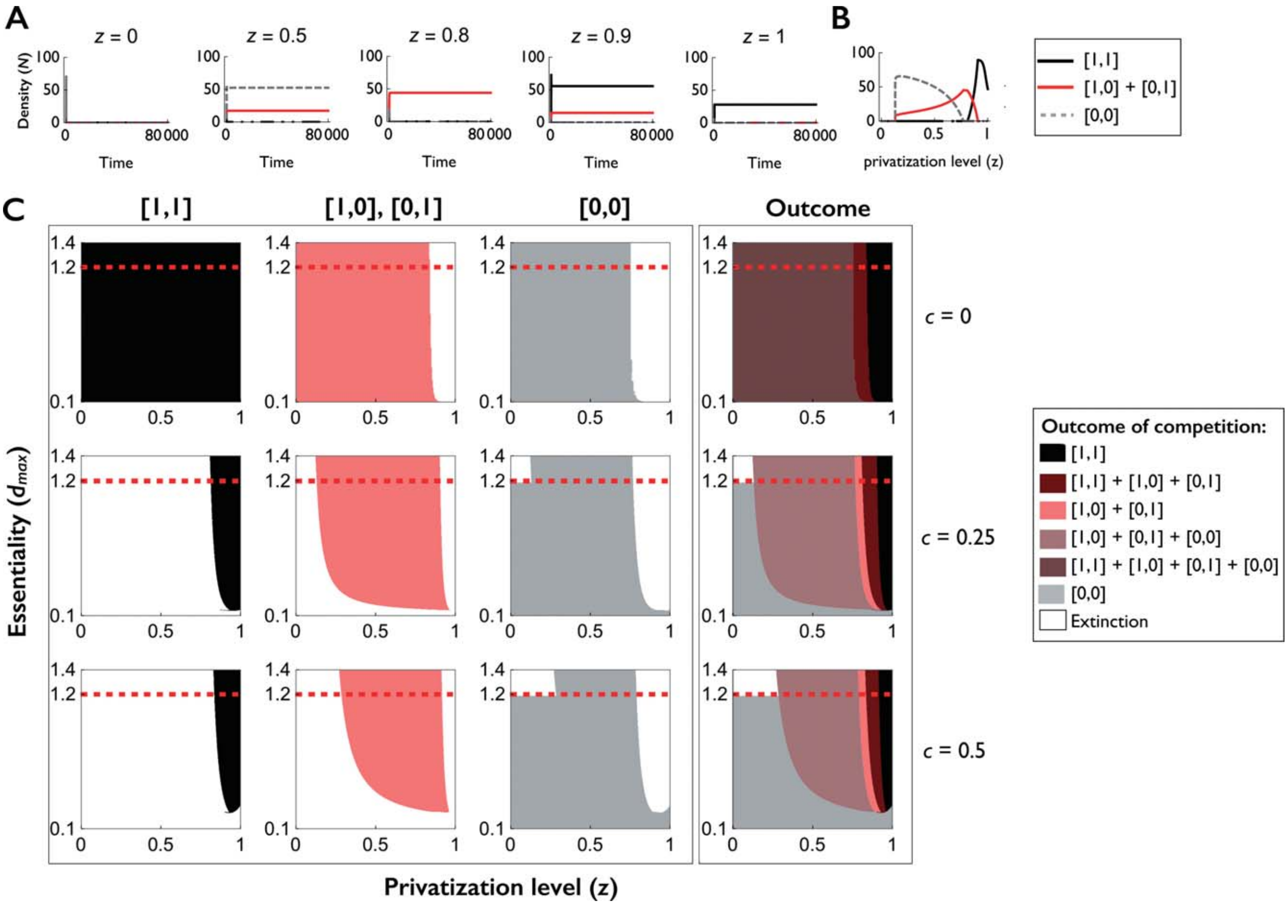

Fig. 2. Effect of privatization level, essentiality and cost on the outcome of interaction.
A. Population densities as a function of time for distinct levels of privatization (z).
B. Equilibrium population densities as a function of the privatization level. Note that the red lines show the density of the single producer [1,0] and overlay the line representing the density of [0,1].
C. For a given cost (c), panels 1–3 show whether the represented genotype is present (coloured) or absent (white) after competition. [1,1] is the double producer, [1,0] and [0,1] are the single producers and [0,0] is the non-producer. The panel 4 shows the outcome of competition (see legend on figure) and is obtained by overlaying panels 1–3. For instance, the pink shading shows the region of the parameter space where the two single producers outcompete the producer and non-producer (i.e., [1,0] + [0,1]). We define extinction as the region where the total population density is lower than 1. The total cost paid by a genotype that performs all functions is c. Above the red line the function becomes strictly essential (i.e. $d_{max} > g_{max}$). All simulations were run for a time $t = 80\,000$ and started with all four genotypes at an initial density $N_i = 5$. Other parameter values: $\gamma = 0.2$, $\theta = 1$, $g_{max} = 1.2$, $d_{min} = 0.1$ and $\varkappa = 100$, and for A and B, $d_{max} = 1.2$ and $c = 0.25$.

essentiality of the functions, with a narrow region of the parameter space where neither double producers nor non-producers are able to invade the mutualism (Fig. 2C), and that is robust to lower initial densities (Fig. S3) and lower production level (Fig. S4). As the level of privatization of the leaky functions increases, the two single producers coexist with the double producer, up to a certain threshold of privatization beyond which the double producer persists alone. In contrast, low privatization favours non-producers, and these can drive the population to extinction (a scenario known as the Tragedy of the Commons; Hardin, 1968) if the benefits from production are mostly public and the function is costly and essential (Fig. 2).

Interplay between community composition and privatization level

Why are the complementary partners favoured at intermediate privatization level? Unlike growing with a single partner, when organisms grow in a diverse community, they face the additional challenge of having to compete with different partners simultaneously. This may impose constraints on an organism's ability to persist because the traits that make a strain a strong competitor against strain *X* may not be the same as the traits that make it a strong competitor against strain *Y*. We suggest that the optimal level of privatization for the two complementary partners depends on whether they share their environment with double producers or non-producers. The reason is that, generally, non-producers are favoured by lower privatization as they reap greater benefits at no cost, whereas producers are favoured by greater privatization because this ensures that they receive a higher share of their production at a reduced risk of being exploited by non-producing types.

To explore this idea, we assume that the two single producers ([1,0] + [0,1]) either compete with the double producer (non-producers absent) or compete with the non-producer (double producers absent). As predicted, we find that equilibrium proportions strongly depend on the degree of privatization (Fig. 3 and Fig. S5). The two single producers are generally favoured by lower privatization when growing with the double producer (Fig. 3A and Fig. S5A) and by greater privatization when growing with the non-producer (Fig. 3B and Fig. S5B), with the caveat that privatization cannot be too low or too high and the function essential, otherwise the system will collapse. This confirms that whether privatization is advantageous or disadvantageous for the mutually interdependent types is context-dependent, strongly depending on the genotypes sharing their environment.

Non-linear benefits from loss affect the outcome of interaction

Interestingly, we have not yet observed the occurrence of pure obligate exploitation (i.e. [1,1] + [0,0]). As seen in the previous section, privatization, cost and essentiality all affect producers and non-producers in opposite directions, which makes a scenario where double producers and non-producers are together less likely. Given this tension, can pure obligate exploitation emerge? So far we have assumed that benefits from loss are linear ($\theta = 1$; Fig. 4A; i.e. the costs increase linearly with the number of

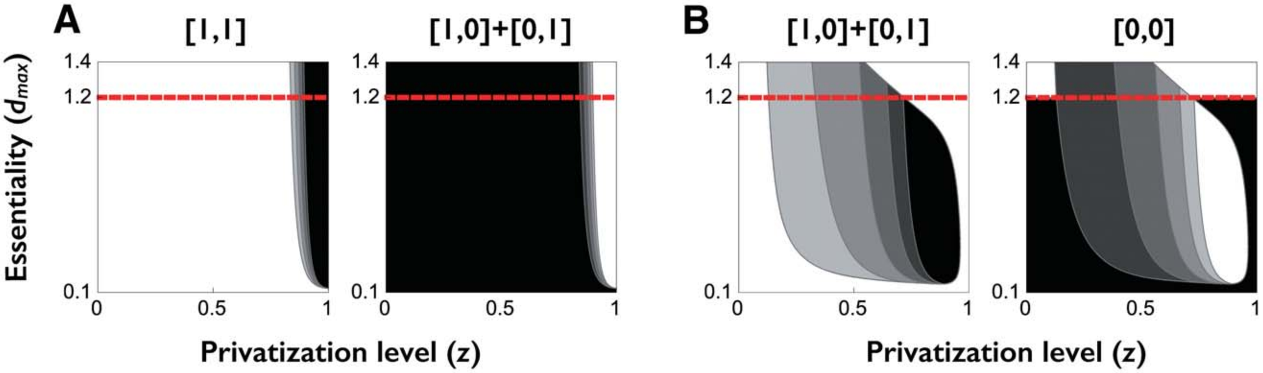

Fig. 3. Effect of privatization level and essentiality on the outcome of 3-strain competition.
A. Community composed of double producers [1,1] and single producers ([1,0] and [0,1]).
B. Community composed of non-producers [0,0] and single producers ([1,0] and [0,1]). The shading shows the proportion of each type (but for [1,0] + [0,1] the shading shows the sum of both proportions). Darker regions represent higher proportions. Above the red line the function becomes strictly essential (i.e. $d_{max} > g_{max}$). In B, above a certain level of privatization and with high essentiality, but not strictly essential, non-producers outcompete the single producers. This likely occurs because the public benefits received are too low to compensate for the costs incurred on growth, and given that the function is not strictly essential, the non-producer outgrows the single producers. $c = 0.25$ and see Fig. S5 for an extended figure with other cost values. For other parameter values used, see Fig. 2 legend.

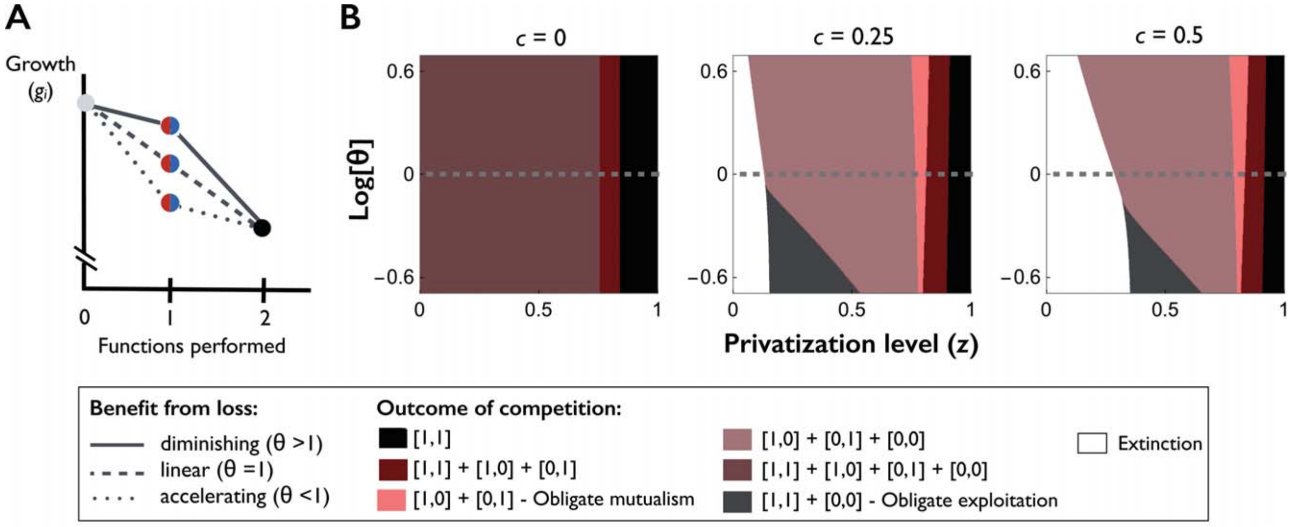

Fig. 4. Non-linear benefits from loss affect the outcome of competition.
A. Consequences for growth of the different shapes of benefits-from-loss of function. We fix the cost paid by double producers to perform two functions (black dot) and vary the cost paid by single producers (red and blue dot). Non-producers grow at a rate g_{max} (grey dot).
B. Effect of privatization level and shape of the benefit from loss of function on the outcome of competition when the functions are essential. For $\log(\theta) = 0$, the benefits from loss are linear; when $\log(\theta) > 0$, the benefits from loss are diminishing; and when $\log(\theta) < 0$, the benefits from loss are accelerating. The total cost paid by a genotype that performs all functions is c. For an explanation of the colour scheme and other parameter values used see Fig. 2 legend.

functions performed, Eq. 1 and Fig. S1A). In other words, the benefit received from losing the first function is identical to the benefit received from losing the second function, which may occur when the two functions are independent. We hypothesize that accelerating benefits from loss (Fig. 4A), i.e. when the benefit from loss of the second function is greater than the benefit from loss of the first function (a scenario called 'Shooting the Moon' in the initial formulation of the BQH; Morris *et al.*, 2012), favours pure obligate exploitation. The rationale behind this hypothesis is that accelerating benefits from loss generates single producers with a reduced growth advantage compared with double producers and an increased growth disadvantage compared with non-producers. Following the same line of reasoning, we expect that diminishing benefits from loss (Fig. 4A), i.e. when the benefit from loss of the first function is greater than the benefit from loss of the second function, favours obligate mutualism. To allow for non-linear benefits from loss, we now vary θ so that when $\theta < 1$ the costs from performing the second function decelerate (i.e. the direct benefits on growth from losing the second function accelerate); and when $\theta > 1$, the costs from performing the second function accelerate (i.e. the direct benefits on growth from losing the second function diminish) (Fig. 4A and Fig. S1A). As predicted, we find that pure obligate exploitation is favoured by accelerating benefits from loss, but only when privatization is low (Fig. 4B). In contrast, diminishing benefits from loss increase the parameter space in which obligate mutualism is favoured (Fig. 4B) (for three-strain competition see Fig. S6). In addition, we find that the obligate mutualism observed here is associated with a marginal increase in community productivity relative to the productivity of a community with double producers only (Fig. S7). This effect becomes stronger as privatization increases and occurs because greater levels of privatization reduce the productivity of double producers (under high-γ scenario; Figs S2 and S7).

Spatial diffusion favours the escape of producers

Another important factor for the evolution of mutualism is spatial structure (Doebeli and Knowlton, 1998; Kim *et al.*, 2008; Harcombe, 2010; Hillesland and Stahl, 2010; Estrela and Brown, 2013; Momeni *et al.*, 2013; Harcombe *et al.*, 2014; Hom and Murray, 2014; Müller *et al.*, 2014; Oliveira *et al.*, 2014). Although spatial structure can favour microbial mutualism because of positive demographic feedbacks between mutually beneficial partners, recent theoretical work suggests that it may hinder the evolution of cooperation between genotypes that exchange multiple secretions (Oliveira *et al.*, 2014). To examine how space affects our findings, we simply extend our well-mixed model to a reaction–diffusion model (see Frank, 1994b, for an example of a spatial extension of a Lotka–Volterra model applied to microbial systems and allelopathy). We assume that strains diffuse across space in a one-dimensional habitat. The reaction–diffusion equation describing the spatial spread of the i^{th} strain in a community with S strains is now given by:

$$\frac{\partial N_i}{\partial t} = D_i\nabla^2 N_i + \left[g_i\left(1-\frac{\sum_{k=1}^{S} N_k}{\varkappa}\right)-d_i\right]N_i \qquad (4)$$

where strain *i* diffuses at a rate D_i and ∇^2 is the Laplacian operator in one dimension (i.e. $\partial^2/\partial x^2$) (Murray, 2003). Note that when $\nabla^2 N_i = 0$ for all *i* (e.g., a spatially homogeneous case), we recover the well-mixed (non-spatial) model. A general finding is that diffusion allows the coexistence of multiple genotypes that are maintained through a spatial polymorphism (Fig. 5 and Fig. S8). A greater level of privatization generally favours invasion by double producers at the moving front, which is likely due to the advantage that privatization confers when a strain invades a new (uncolonized) habitat from rarity (Fig. S8). In contrast, low privatization favours non-producers, but they cannot invade alone and so their speed is limited by the speed of producers (Fig. S8). At intermediate levels of privatization, single producers are able to invade if the benefits from loss are diminishing (Fig. 5C). Given that they move at a faster speed than non-producers, they will escape from non-producers and dominate the system at the moving front (Fig. 5C). After the moving front passes through any given point in space, diffusion plays a negligible role over time, and that point will eventually approach the equilibrium of the well-mixed system.

Discussion

Our main goal here was to explore the drivers of metabolic interdependencies. Why do organisms lose a function that leaves them dependent on other organisms for growth rather than perform the function themselves? What conditions favour the emergence of metabolic complementarity through mutual interdependency rather than one-way exploitation? Focusing on a scenario where two functions may be lost, we found that the level of privatization of the leaky functions is a key factor shaping the outcome of microbial interactions. In particular, we found that mutual interdependency is favoured for a broad range of privatization level, costs and essentiality, but usually persists in association either with organisms that cannot

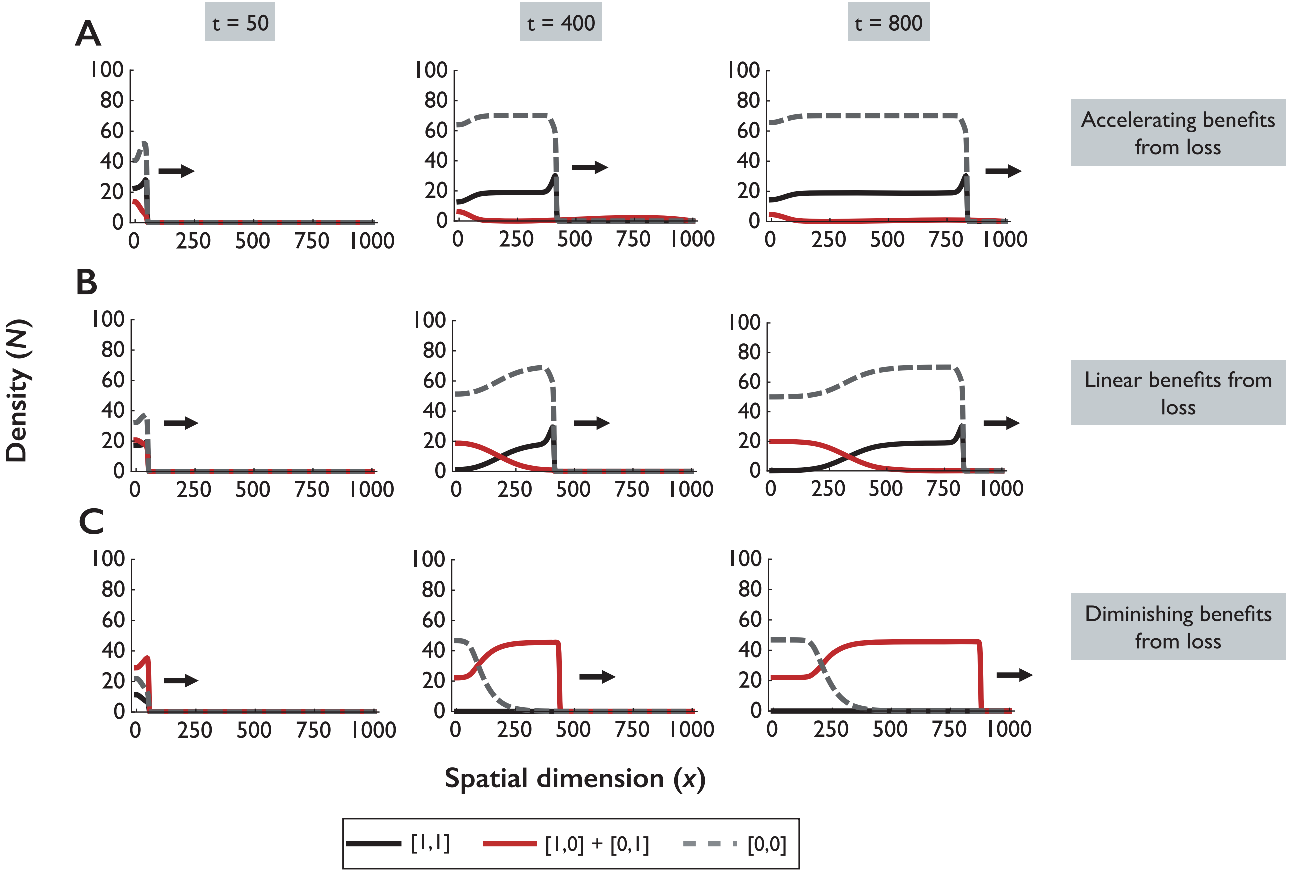

Fig. 5. Effect of strains diffusion on the emergence of microbial interdependencies. Plots show the travelling waves across a one-dimensional spatial habitat (*x*) at different times (*t*) for (A) accelerating, (B) linear and (C) diminishing benefits from loss ($\theta \in \{0.5, 1, 2\}$, respectively). Arrows indicate the direction of travel. The red lines show the density of the single producer [1,0] and overlay the line representing the density of [0,1]. Functions are essential and partially privatized ($z = 0.5$). $c = 0.25$, $D = 1$. For other parameter values used see Fig. 2 legend.

perform any of the functions (for lower privatization) or with organisms that perform all of the functions (for higher privatization). When privatization is extremely high, however, double producers persist alone and exclude the single producers and non-producers because the public benefits are too low to support their growth.

How can these different levels of benefits across the public–private continuum be achieved physiologically? A potential explanation lies in the diversity of mechanisms by which microbes can partially privatize their produced goods (Morris, 2015). For instance, some microbes partially privatize their goods by producing and keeping them intracellularly, thus any public benefit arises purely from 'leakiness'. An example of this is the unavoidable detoxification of extracellular hydrogen peroxide (H_20_2) (Morris *et al.*, 2014). Although H_20_2 is detoxified intracellularly (hence private) because the detoxifying enzyme catalase is not released into the extracellular environment, the cellular membrane is highly permeable to H_20_2, thus resulting in the diffusion of H_20_2 into the cell and consequent detoxification of the extracellular (hence public) environment. Alternatively, microbes can partially privatize enzymes by producing and keeping them in their cell wall or near their cell surface. For example, sucrose is hydrolysed into simple monossacharides by invertase located in the cell wall. The monossacharides are then imported into the cell, but some will eventually diffuse away from the producer cell and become available to neighbouring cells (Gore *et al.*, 2009). Another mechanism of privatization is when the molecule is released into the extracellular environment but then adheres to the producer cell (e.g., putisolvin biosurfactants; Cárcamo-Oyarce *et al.*, 2015). Given these distinct mechanisms of privatization, one could speculate that products that are kept intracellularly lie near the private end of the continuum, whereas products that are released extracellularly lie near the public end of the continuum. But whether this is correct and what the implications of these different physiological mechanisms for the evolutionary trajectory of interdependencies are remain to be explored. Note that these physiological mechanisms of partial privatization are different from a type of privatization that arises because of the physicochemical properties of the environment, such as the diffusion properties of the secreted molecules or the level of habitat structure (e.g., biofilm versus planktonic growth) (Kümmerli *et al.*, 2014).

In our model, linear benefits from loss indicate that there is a constant increment in gain from further losses. Assuming, for instance, two functions, this means that the gain received from losing the second function is the same as the gain received from losing the first function. Relaxing this assumption, we found that different shapes of the benefit-from-loss function lead to different outcomes. Specifically, accelerating benefits from loss favour one-way dependency (obligate exploitation), whereas diminishing benefits from loss favour mutual interdependency (obligate mutualism). Non-linear benefits from loss can occur because of epistatic interactions between different metabolic functions. For instance, when two functions share a common branched pathway, they share metabolic intermediates, thus the loss of the first function may provide a lower benefit than the loss of the second function due to the maintenance cost of the shared metabolic pathway (accelerating benefits from loss). By contrast, diminishing benefits from loss arise because of metabolic conflict between functions because of, for example, competition for a shared limiting intracellular resource (Johnson *et al.*, 2012). Under this scenario, the loss of the first function removes the competition for the limiting resource, and as a consequence, that resource can be diverted to a single function rather than split between two functions. Building on the idea that metabolic conflicts are important for the evolution of metabolic specialization (Pfeiffer and Bonhoeffer, 2004; Johnson *et al.*, 2012), we argue that they are also key to the evolution of microbial interdependencies. Whether evolution by natural selection favours few keystone organisms producing a function that many other partners rely upon (the 'shooting the moon' strategy in the BQH; Morris *et al.*, 2012) or more even interactions where partners trade complementary functions very likely depends on the interplay between costs and the type of the interaction between lost functions.

For simplicity, here we have assumed that all biological functions have identical properties, including identical costs, essentiality and privatization levels. Distinct functions, however, may carry distinct properties. For instance, different amino acids have different biosynthesis costs (Mee *et al.*, 2014). Additionally, epistasis with other components of the genome may alter the cost of the same function expressed by different organisms with different levels of loss. Asymmetries in costs of performing functions can potentially lead to a scenario where one partner performs a single high-cost function (and has lost multiple low-cost functions), whereas the complementary partner performs multiple low-cost functions (and has lost the high-cost function) and may also influence the likelihood of special scenarios such as 'Shooting the Moon'. More generally, we believe that asymmetries in function properties are likely to play an important role in shaping the trajectory of loss of functions and consequent emergence of microbial dependencies, particularly in more complex communities.

Our model explores the dynamics of genotypes that interact over an ecological timescale with the primary goal of gaining new insight into the origin of microbial interdependencies. Although not the scope of this study, it would be interesting to explore the evolutionary trajectory of such microbial interactions. For instance, it has been suggested that the loss of methionine biosynthesis by

Escherichia coli may lead to the overproduction of threonine (and vice versa), which may explain the synergistic growth observed between methionine and threonine auxotrophs (Mee *et al*., 2014). Given such positive feedbacks, one may ask whether this could lead to the evolution of partner specialization through partner fidelity feedback (Bull and Rice, 1991; Sachs *et al*., 2004; Foster and Wenseleers, 2006).

Finally, we explore how space affects our findings by extending our well-mixed model to a reaction–diffusion model. Our findings suggest that spatial diffusion generally favours double producers at the expense of single producers and non-producers. This is consistent with recent theoretical work showing that spatial structure favours within-genotype cooperation (double producer alone in our model), whereas it disfavours between-genotype cooperation (the two single producers in our model) because the local diffusion of secretions prevented the complementary genotypes from interacting (Oliveira *et al*., 2014). Also, work focusing on the evolution of within-species cooperation showed that range expansion can, under some conditions, promote cooperation by allowing cooperators to invade and colonize new empty territories faster than non-cooperators (Datta *et al*., 2013; Korolev, 2013; Van Dyken *et al*., 2013). Interestingly, we also find that, under some conditions, the two single producers are able to escape from non-producers and double producers by finding refuge at the moving front of the spatially expanding community, a result that may be particularly relevant to bacterial communities undergoing spatial expansions as when communities grow on agar plates (Korolev *et al*., 2011). Our spatial model takes the first natural step to build a spatial dimension into our well-mixed model because we only add the diffusion of strains as a new component in the model. This approach provides us with a rigorous way to capture the effect of introducing space while using our well-mixed model as a control. Further enrichments of the model (e.g., explicit diffusion of the public good or discreteness of individual cells) could also be incorporated, for instance using an individual-based modelling approach (Oliveira *et al*., 2014). It should be noted that, under some conditions, varying privatization level may have a similar effect as varying diffusion rates of the produced good. However, a key feature of our model is that it captures biological systems where the partial privatization of benefits may be achieved through a physiological mechanism (e.g., physical barrier of the cell wall). This mechanism of privatization is crucial to ensure that producers retain their private benefits not only when they are rare, but also when environmental diffusion is high. And, importantly, such private benefits may ultimately be essential to prevent the breakdown of microbial interdependencies that arise through loss of function.

In summary, our results suggest that mutual interdependency is more likely to arise for essential functions that are partially privatized. Crucially, this offers an additional mechanism by which mutual interdependency can be maintained without the need for spatial structure or any particular feature of the life cycle of microbes, such as population bottleneck size (Oliveira *et al*., 2014), and this may help explain, for instance, the existence of microbial dependencies in marine environments. Most likely, these factors will act in combination, and understanding this interplay may be key to understanding how microbial interdependencies arise and are maintained in diverse habitats.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Illustration of the functional forms used in the model. (A) Cost ($c_i = g_{max}$- g_i, see eq. (1)) and growth (g_i) as a function of the number of biological functions performed. When $\theta = 1$, costs increase linearly with increasing number of functions performed; when $\theta < 1$, costs decelerate (i.e. accelerating benefits from loss); and when $\theta > 1$, costs accelerate (i.e. diminishing benefits from loss). (B) Death function (d_i) of double producers alone as a function of the number of producers (N). Levels of privatization vary from fully public ($z = 0$, lighter grey line) to partially privatized ($z = 0.5$, darker grey line) to fully private ($z = 1$, black line). For $\gamma = 0.2$ (parameter value considered in our model analysis), we can see that as the number of producers increases, the death rate decreases exponentially to d_{min} ($d_{min} = 0.1$). In addition, higher privatization leads to lower death rate when the density of producers is low but to higher death rate when the density of producers is high (as the death function decreases more quickly for lower privatization). This shows that greater privatization is favoured when producers are rare, unless the public/private effectiveness factor (γ) is very high (right panel). When γ is very low (left panel), greater privatization is favoured for $N < \varkappa$ (i.e., $N < 100$). As expected, when the good is fully private (i.e. $z = 1$), the death rate is independent of the number of producers. Here $\theta = 1$.

Fig. S2. Effect of privatization level and cost on the double producer alone. (A) Density of double producer [1,1] as a function of privatization level (z) and for varying cost (c, cost increases from light to dark) and public/private effectiveness factor (γ). (B) Double producer growth ($g_{[1,1]}$) and death ($d_{[1,1]}$) functions. When the two surfaces intersect (black thick line) we have an equilibrium. If the green surface ($g_{[1,1]}$) starts above the yellow surface ($d_{[1,1]}$), we have a stable equilibrium (N^*). We can see that a rare producer cannot invade from rare when privatization is low and that the minimum density of invasion from rare increases as privatization decreases and cost increases. $\gamma = 0.2$. For other parameter values used see Fig. 2 legend.

Fig. S3. Effect of decreasing the initial densities on the outcome of interaction. Lower initial densities reduce the regions of the parameter space where the system can persist, in particular regions where the system is generally supported by single producers (Fig. 2C). In line with our findings for double producers growing alone (Fig. S2), invasion from rare is favoured by higher privatization levels and lower costs. Here the simulations were started with all four genotypes at an initial density $N_i = 1$.For other parameter values, see Fig. 2C.

Fig. S4. Effect of intermediate levels of performing the functions. Here the genotypes become [0.5, 0.5] for double producers, [0.5, 0] and [0, 0.5] for the single producers, and [0, 0] for non-producers (i.e., $a_{i,j} \in \{0, 0.5\}$). As in the model where $a_{i,j} \in \{0,1\}$, single producers are favoured at intermediate level of privatization. However, their coexistence with double producers only or full extinction is now increased. For other parameter values, see Fig. 2C.

Fig. S5. Effect of privatization level and essentiality on the outcome of the 3-strain competition. (A) double producer and two single producers. (B) two single producers and non-producer. The shading shows the proportion of each type (for [1,0]+[0,1] the shading shows the sum of both proportions). Darker regions represent higher proportions. Above the red line the function becomes strictly essential (i.e. $d_{max} > g_{max}$). For other parameter values used see Fig. 2 legend.

Fig. S6. Effect of privatization level and shape of benefit from loss function on the outcome of the 3-strain competition. A. double producer and two single producers. B. two single producers and non-producer. Functions are strictly essential. For $\log(\theta) = 0$, the benefits from loss are linear; when

$\log(\theta) > 0$, the benefits from loss are diminishing; and when $\log(\theta) < 0$, the benefits from loss are accelerating. The total cost paid by a genotype that performs all functions is c. For other parameter values used see Fig. 2 legend.

Fig. S7. Densities as a function of privatization for the 4-strain competition. The dashed purple line shows the productivity of the community, and the red line shows the sum of the densities of the two single producers. When essential functions are costly to perform, communities with single producers only are marginally more productive than communities with double producers only. This effect becomes stronger as privatization increases and occurs because greater privatization harms double producers community productivity (Fig. S2). (A) Accelerating; (B) linear; and (C) diminishing benefits from loss ($\theta \in \{0.5, 1, 2\}$, respectively). For other parameter values used see Fig. 2 legend.

Fig. S8. Effect of privatization level and shape of benefit from loss of function on the outcome of the 4-strain competition when there is no spatial diffusion (A) or spatial diffusion (B). Levels of privatization vary from fully public ($z = 0$, top row) to fully private ($z = 1$, bottom row). Accelerating (left column), linear (middle column) and diminishing (right column) benefits from loss. The red line shows the density of the single producer [1,0] and overlays the line representing the density of [0,1]. In (B), $t = 1000$ except if noted otherwise. $c = 0.25$; $D = 1$.