Axiomatic Ecology: Rules for Building Consistent Ecosystem Models

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Non-mechanistic ecosystem models are employed in many ecological studies ranging from purely theoretical to data-driven ones. With such models in mind, we derive fundamental consistency criteria *(axioms)* from first principles. These particularly cover what we call *clone consistency:* The outcome does not change if a population is split into two with identical properties. We mathematically prove that, these axioms are fulfilled if and only if the model is based on linear combinations of powers of parameters and abundances. Using this insight, we formulate a framework that allows to quickly assess the consistency of existing models and to build new models. We demonstrate our approach by invalidating a data-based model proposed for polymicrobial urinary-tract infections and developing an alternative. We argue that our framework reveals implicit assumptions and informs the general modelling studies by narrowing the space of possible models or pointing to new forms of models.

I. INTRODUCTION

Many theoretical and semi-empirical modelling studies of ecological communities employ general models [1–3], such as the popular Volterra model [4]. Such models are often not mechanistic or process-oriented, i.e., they do not explicitly feature agents of interactions, such as nutrients and toxins. As a result the equations governing each population all have the same form, and the species of a population only manifests in the values of the associated control parameters. These parameters may describe the properties of a single population, the interplay of two populations, or higher-order interactions, i.e., effects involving three or more populations [5, 6]. They are usually chosen randomly [7–12] or determined from experiment [13–16].

In particular for microbial ecosystems, recent advances in automatising experiments have made it feasible to determine interaction parameters for richer ecosystems [15, 17–19], to quantify the interaction between two populations with more than one parameter [15], or to measure higher-order interactions [14, 20]. These new experimental scenarios often demand new models that can incorporate the respective data, in particular as there is no single answer as to how multi-parameter or higher-order interactions should be measured [2, 6, 15, 18, 21].

One difficulty when building a model is to avoid inconsistencies. As an example, we compare two simulations of a bacterial community using the same model (Box 1): The first simulation is straightforward; we represent each strain of bacteria as one population. For the second simulation, we divide one population into two with identical properties. Allegorically, we paint half the individuals in a different colour. Although these two simulations describe an identical situation, their outcomes strongly differ (Fig. 1, solid and dashed lines), which is why we consider the model underlying these simulations as inconsistent. This difference cannot be explained by numerical noise and sensitivity to initial conditions, as demonstrated by simulations with perturbed initial conditions (dotted lines) exhibiting a much smaller difference. This model was taken from a study [15] that featured communities containing two strains of the same species; therefore the case of populations with very similar properties is relevant here.
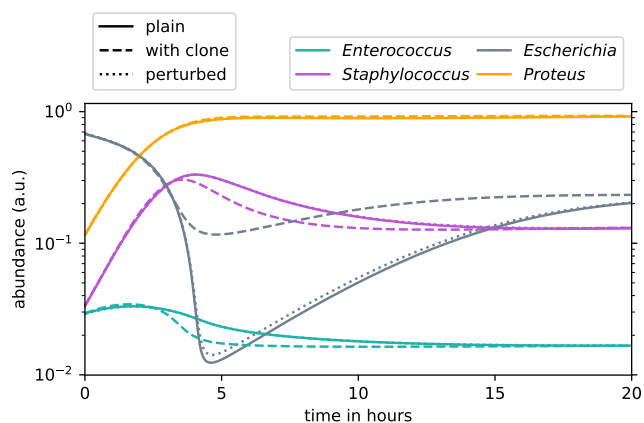

FIG. 1. Simulation of a urinary-tract-infection community (Community 3 from Ref. 15) using Eq. 1 from Box 1. Solid lines: plain simulation; each strain is represented by one population. Dashed lines: the same, except that there are two *Enterococcus* populations with identical parameters and half the initial abundance each. The abundance shown for *Enterococcus* is summed over these two populations. Dotted lines: like plain simulation, except that the initial abundances were perturbed by 1 % in a random direction. (A dotted line may be mostly covered by the respective solid line.) See Appendix A for details of the simulation.

In Appendix B we provide an explicit arithmetic demonstration of this inconsistency that is independent of some choices we had to make for this example (see Appendix A).

We here formulate criteria *(axioms)* that exclude such fundamental inconsistencies. Applying methods from functional analysis, we explore the consequences of these axioms and derive a framework that allows to easily decide whether a given model is consistent and to build models that are. We demonstrate the latter by building a new semi-empirical model for polymicrobial urinary-tract infections. Moreover, we argue that our theoretical results are relevant to all kinds of ecosystem models and may inform them with respect to their consistency or implicit assumptions required to maintain this consistency.

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Box 1. **Our Case Study: Semi-Empirical Models of Urinary-Tract Infections**

Ref. 15 used a high-throughput approach to systematically measure ecological interactions between strains isolated from polymicrobial urinary-tract infections (UTI). Employing this data, Ref. 15 also proposed a model for ecosystems consisting of such strains. We use this scenario and the model as an example for applying our concepts.

We briefly summarise the measurements of the growth characteristics and pairwise interactions of these bacterial strains:
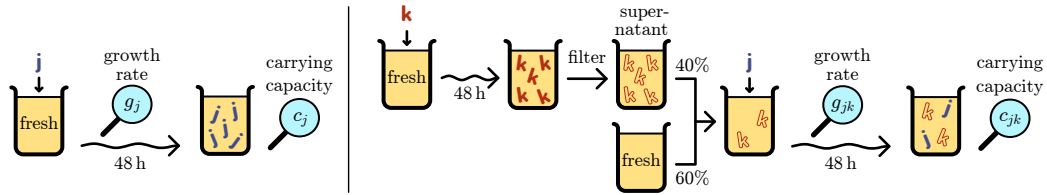
Left: Each strain j was cultivated for $48\,\mathrm{h}$ in artificial urine (solid bold letters represent individuals of the respective strain). The exponential growth rate g_j as well as the carrying capacity c_j (named *yield* in Ref. 15) were experimentally determined via optical densities. For convenience, abundances of each strain were normalised such that $c_j = 1$. Right: Moreover, for each strain k, a conditioned medium was produced by letting the strain grow for $48\,\mathrm{h}$, mechanically removing the bacteria to obtain a *supernatant,* (represented by outline letters) and mixing the result with fresh medium in a ratio of $v := 0.4$. In each such medium, each strain j was cultivated, and the conditioned growth rate g_{jk} and carrying capacity c_{jk} were determined as above.

In the model proposed by Ref. 15 using this data, the (normalised) abundance x_j of population j is described by the following differential equation (with $\lceil z \rceil := \max(0, z)$):

$$\dot{x}_j = x_j\, g_j \underbrace{\left[1 + \sum_{k \neq j} a_{jk} x_k\right]}_{\text{growth term}} \underbrace{\left(1 - \frac{x_j}{\left\lceil 1 + \sum_{k \neq j} b_{jk} x_k \right\rceil}\right)}_{\text{capacity term}}, \tag{1}$$

with $a_{jk} := \dfrac{g_{jk}}{g_j} - 1$ and $b_{jk} := \begin{cases} c_{jk} - 1 & \text{if } c_{jk} \geq 1 \\ \frac{1}{v}(c_{jk} - 1) & \text{if } c_{jk} < 1 \end{cases}$.

II. IMPACT FUNCTIONS

We consider functions that describe the impact of an ecosystem consisting of n populations on a species in that ecosystem, a resource, or similar. Examples of phenomena described by such *impact functions* include:

- the effective growth rate of a given species

- the remaining size of a niche,

- the availability of some nutrient,

- reproductive services, e.g., pollination.

The arguments of these functions are the abundances of all populations in that ecosystem and m parameters per population quantifying its impact.

Before we formulate our criteria, we formalise this scenario and introduce some helpful notational conventions: We denote by $X = \mathbb{R}^n_+$ the space of all possible population abundances, where $\mathbb{R}_+$ denotes the non-negative real numbers. Also, we denote by $A = \mathbb{R}^{n \times m}$ the space of all possible parameter configurations of these populations. The domain of impact functions is thus $X \times A$. Furthermore, we denote an arbitrary pair of arguments for impact functions by $(\mathbf{x}, \mathbf{a})$, where $\mathbf{x} := (x_1, \ldots, x_n) \in X$ and $\mathbf{a} := (a_1, \ldots, a_n) \in A$ with $a_i \in \mathbb{R}^m$ being the parameter values that describe population i. In general, lowercase italic letters denote numbers or parameter configurations (tuples of numbers); Greek letters denote functions; boldface letters denote vectors or similar; uppercase letters denote sets of respective contents. Finally, we use non-italic sans-serif letters to identify modifications of specific components of arguments of these functions (similar to named arguments in many programming languages)
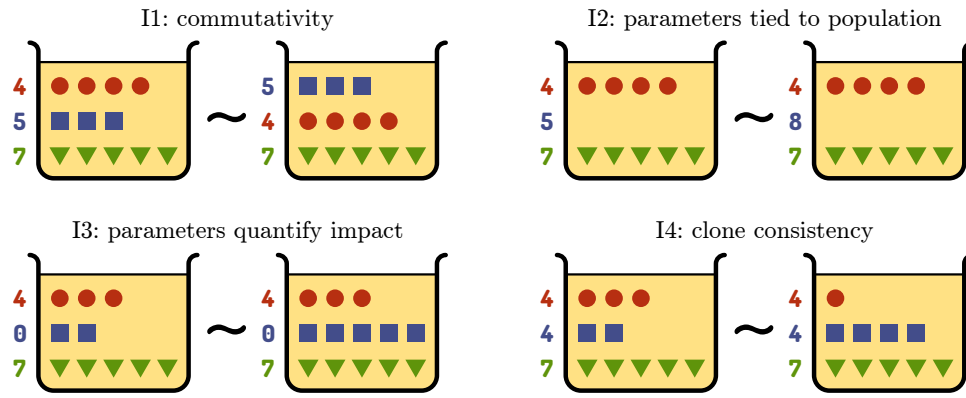
FIG. 2. Examples of the axioms that we require impact functions to fulfil. Circles, squares, and triangles represent individuals of different populations. Numbers on the left of the vats represent the parameter governing the respective population. The similar sign ($\sim$) indicates that two situations are equivalent as arguments of an impact function, i.e., they should yield the same result.

to obtain notational abbreviations like the following:

$$\phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_2 = y) := \phi((x_1, y, x_3, \ldots, x_n), (a_1, \ldots, a_n)).$$

Here the arguments of the function ϕ are $\mathbf{x}$ and $\mathbf{a}$ except for the abundance of the second population (x_2) being changed to y.

A. Ensuring Consistency

As our requirements have a very broad scope of application and to distinguish them from model-specific criteria, we call them *axioms*. The axioms we require an impact function $\phi : X \times A \to \mathbb{R}$ to fulfil are:

I1: There are no population-specific mechanisms in the general form of the model – the properties of a given population are completely captured by its associated parameters. A specific model can still feature population-specific mechanisms, e.g., when a specific parameter has a value of 0 for all but one populations (also see Axiom I3). This way, the axiom can also be fulfilled by a typical mechanistic model.

Codifying this axiom mathematically, the order of populations does not matter, and the impact function does not change when parameters and populations are swapped simultaneously (Fig. 2, top left):

$$\phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_i = x_j, \mathsf{x}_j = x_i, \mathsf{a}_i = a_j, \mathsf{a}_j = a_i)$$
$$= \phi(\mathbf{x}, \mathbf{a}) \qquad \forall i \neq j.$$

Following mathematical nomenclature, we refer to this axiom as *commutativity*.

I2: Parameters describe only their associated populations. Hence, when a population is absent, the associated parameters have no effect (Fig. 2, top right):

$$\phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_1 = 0, \mathsf{a}_1 = a_1)$$
$$= \phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_1 = 0, \mathsf{a}_1 = b_1) \qquad \forall a_1, b_1 \in \mathbb{R}^m$$

I3: Parameters quantify the impact of the associated population and are scaled such that all parameters associated to a given population being zero corresponds to no impact of that population (Fig. 2, bottom left):

$$\phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_1 = x_1, \mathsf{a}_1 = 0)$$
$$= \phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_1 = y_1, \mathsf{a}_1 = 0) \qquad \forall x_1, y_1 \in \mathbb{R}_+$$

Note that while we chose zero as the parameter value corresponding to no impact, it is straightforward to translate our results to any other choice of this constant.

I4: Suppose two populations have identical parameter values. This means that they feature identical individuals (clones) within the limitations of the model. Then the impact of these two populations should only depend on their total abundance, and not on how it is distributed onto the two populations (Fig. 2, bottom right):

$$\phi(\mathbf{x}, \mathbf{a}, \mathsf{x}_1 = x_1 + z, \mathsf{x}_2 = x_2 - z, \mathsf{a}_1 = \mathsf{a}_2 = b)$$
$$= \phi(\mathbf{x}, \mathbf{a}, \mathsf{a}_1 = \mathsf{a}_2 = b) \qquad \forall z \in [-x_1, x_2]$$

If this requirement is not fulfilled, the resulting model can produce different outcomes when implementing the same scenario in different ways, as exemplified in Fig. 1. We refer to this axiom as *clone consistency*.

Note that through commutativity (I1), the other axioms apply to all arguments or pairs of arguments, respectively. Also, clone consistency (I4) of more than two populations is covered by applying the respective axiom repeatedly. Furthermore note that the above axioms do not explicitly capture (but also do not exclude) the case that a parameter is associated with more than one population, which is relevant for a higher-order interaction.

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<div align="center">Box 2. The Functional Algebra of Impact Functions</div>

In this box we explain the mathematical concepts of the following theorem and provide the main parts of a proof:

Theorem 1. *Let $\Lambda_k := \left\{ \mathbf{x}, \mathbf{a} \mapsto \sum_{i=1}^{n} a_{ki}^{j} x_i \,\middle|\, j \in \{1, \ldots\} \right\}$ denote the set of linear combinations of powers of values of the k-th parameter and abundances. Denote the set of all such functions as $\Lambda = \bigcup_{i=1}^{m} \Lambda_i$. Let $\Xi := \Lambda \cup \Gamma$, where Γ is the set of constant functions. Let Φ be the smallest closed functional algebra that contains Ξ. Then Φ contains all impact functions.*

That the impact functions form a functional algebra Φ means that each product or sum of two impact functions is again an impact function and that each multiple of an impact function is an impact function. This algebra being closed means that the limit of uniformly converging sequences of impact functions is again an impact function.

Φ being the smallest such algebra containing Ξ means that all impact functions can be built from elements of Ξ using addition, multiplication, and taking a limit. In mathematical terms, Φ is the *generated set* of Ξ, and conversely, Ξ is the *generating set* of Φ, where taking the limit of a uniformly converging sequence is considered amongst the generating operations.

To prove Theorem 1, we apply Bishop's Theorem [22, 23], which states, when reduced to algebras of real-valued functions:

Bishop's Theorem. *Let Z be a compact Hausdorff space. Let Ψ be a closed unitial subalgebra of $C(Z, \mathbb{R})$. Let $\phi \in C(Z, \mathbb{R})$. Suppose that $\phi|_S$ is constant for each subset $S \in Z$ such that $\psi|_S$ is constant for all $\psi \in \Psi$. Then $\phi \in \Psi$.*

As Z can be any sufficiently large compact subset of $X \times A$, we can identify Ψ with Φ, i.e., the generated set of Ξ. *Unitial* means that the functional algebra shall contain the constant functions, which is fulfilled by construction for Ψ. Thus, to show that the functional algebra Ψ contains all impact functions, it only remains to be shown that for an arbitrary impact function ϕ for any $\mathbf{x}, \hat{\mathbf{x}} \in X$ and $\mathbf{a}, \hat{\mathbf{a}} \in A$:

$$\psi(\mathbf{x}, \mathbf{a}) = \psi(\hat{\mathbf{x}}, \hat{\mathbf{a}}) \; \forall \psi \in \Psi \quad \implies \quad \phi(\mathbf{x}, \mathbf{a}) = \phi(\hat{\mathbf{x}}, \hat{\mathbf{a}}),$$

or, in the language of functional analysis, Ψ has to *point-separate,* except where impact functions do not point-separate either. Since point-separations are unaffected by algebraic operations of functions and limits, Ψ is point-separating, if and only if Ξ is. Moreover, since the functions form Γ are constant everywhere (and thus point-separating nowhere), this is equivalent to Λ being point-separating. Finally, since for any $i \neq j$, the functions from Λ_i are constant wherever the functions from Λ_j are not, it suffices to consider one Λ_i only. This case in turn is covered by the following lemma, which we prove in Appendix C:

Lemma 1. *Suppose $\mathbf{x}, \hat{\mathbf{x}} \in X$ and $\mathbf{a}, \hat{\mathbf{a}} \in A$ are such that: $\sum_{i=1}^{n} a_i^{j} x_i = \sum_{i=1}^{n} \hat{a}_i^{j} \hat{x}_i \; \forall j \in \{1, \ldots\}$. Let ϕ be an impact function. Then $\phi(\mathbf{x}, \mathbf{a}) = \phi(\hat{\mathbf{x}}, \hat{\mathbf{a}})$.* □

Examples of impact functions that will be important in the remainder of the paper are:

- Linear combinations of parameter values and abundances: $\mathbf{x}, \mathbf{a} \mapsto \sum_{i=1}^{n} a_i x_i$, where $\mathcal{Y} \mapsto \mathcal{Z}$ denotes the function that maps $\mathcal{Y}$ to $\mathcal{Z}$. These are for example featured in the interaction term of most variations of the Volterra model [4].

- Constant functions: $\mathbf{x}, \mathbf{a} \mapsto h$, with $h \in \mathbb{R}$. These cover the case that some quantity is not influenced by the ecosystem at all.

B. Basic Building Blocks of Ecosystem Models

In Box 2 we state and prove a theorem on the composition of impact functions, which facilitates testing whether models comply with the axioms and building models that do. It has two important implications for modelling:

The first is that everything built from impact functions via addition, multiplication, function composition, etc. is again an impact function, formally: If $\phi_1, \ldots, \phi_l$ are impact functions and $\chi : \mathbb{R}^l \to \mathbb{R}$ is an arbitrary function combining the

results of these impact functions, then:

$$\mathbf{x}, \mathbf{a} \mapsto \chi(\phi_1(\mathbf{x}, \mathbf{a}), \ldots, \phi_l(\mathbf{x}, \mathbf{a})),$$

is also an impact function. As an illustrative example consider a population that can diauxically live on two nutrients P and Q with efficiency e_P and e_Q. On the one hand, we can use two impact functions γ_P and γ_Q to describe the concentrations of these nutrients in dependence of the other populations in the ecosystem that produce or consume them. On the other hand, we can also use the impact function $\mathbf{x}, \mathbf{a} \mapsto e_P \gamma_P(\mathbf{x}, \mathbf{a}) + e_Q \gamma_Q(\mathbf{x}, \mathbf{a})$, which describes how much our population can grow on the nutrients provided by the ecosystem.

The other implication of the theorem is that all impact functions can be written using (possibly infinitely many) elements from a set Ξ of basic building blocks, namely linear combinations of powers of parameter values and abundances and constant functions. Conversely, all models complying with our axioms must be decomposable into these basic building blocks. For application, it is arguably more convenient to use the equivalent set of basic building blocks that have the form:

$$\mathbf{x}, \mathbf{a} \mapsto \zeta\left(\sum_{i=1}^{n} \kappa(a_i) x_i\right), \tag{2}$$

where $\zeta : \mathbb{R} \to \mathbb{R}$, $\kappa : \mathbb{R} \to \mathbb{R}$ with $\kappa(0) = 0$. Here, the functions ζ and κ may comprise infinite series of elements from Ξ, thus simplifying the representation. On the other hand, all elements from Ξ can be represented in this form. We refer to these as *basic impact functions* from now on.

A corresponding basic building block featuring general second-order interactions is:

$$\mathbf{x}, \mathbf{a} \mapsto \zeta\left(\sum_{i=1}^{n}\sum_{j=1}^{n} \kappa(a_{ij}) x_i x_j\right), \tag{3}$$

which is an impact function no matter whether a_{ij} is considered a parameter associated to population i or to j. Analogous building blocks exist for even higher interaction orders. Such building blocks are featured in existing models of higher-order interactions [11, 12, 16].

Many ecosystem models feature a change of abundances, having forms like $\dot{x}_j = \mathcal{R}_j(x_j)$ or $x_j(t+1) = x_j(t) + \mathcal{R}_j(x_j(t))$. If we assume for simplicity's sake that there is no delay, noise, or similar, we can write the right-hand side $\mathcal{R}$ of the equation in the form:

$$\mathcal{R}_j(x_j) = \beta_j(x_j, \phi_j(\mathbf{x}, \mathbf{a}))$$

with $\beta_j : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$. If, similar to Axiom I4, we consider the case of two populations j and k with identical properties with abundances y and z, their total growth must be the same as if all individuals were assigned to one population:

$$\mathcal{R}_j(y) + \mathcal{R}_k(z) = \mathcal{R}_j(y+z) + \mathcal{R}_k(0) = \mathcal{R}_j(y+z).$$

Using that j and k are identical as well as the properties of impact functions, we can conclude from this that:

$$\beta_j(y, w) + \beta_j(z, w) = \beta_j(y+z, w),$$

with $w = \phi_j(\mathbf{x}, \mathbf{a}, \mathsf{x}_j = y + z, \mathsf{x}_k = 0)$. Therefore β must be proportional in its first argument. Practically this means that all dependencies of $\mathcal{R}_j$ on $\mathbf{x}$ must either happen within an impact function or in the form of a single factor x_j.

We can now easily verify for most models whether they comply with our consistency requirements by checking whether they are built from impact functions. This in turn we can do by looking for terms of the above form (Eq. 2). For instance, the Volterra model [4] (with the carrying capacity for each population normalised to 1) can be rewritten as follows:

$$\dot{x}_j = g_j x_j \left(1 - x_j - \sum_{k \neq j} a_{jk} x_k\right) = g_j x_j \left(1 - \sum_{k} a_{jk} x_k\right),$$

with $a_{jj} = -1$. This is clearly built from a linear combination and a factor x_j and we can thus be sure that it complies with our axioms.

In another example, we can look at the model given by Eq. 1 from Box 1 within our framework: Both the capacity and growth term correspond to impact functions, and a and b are the parameters quantifying these impacts. However, it is clear that neither is built from linear combinations (with complete sums). From this, we can deduce that the model violates at least one of our axioms. Since it clearly fulfils Axioms I1–I3, it must fail to be clone-consistent (Axiom I4), which we observed in Fig. 1. Note that completing the sums with appropriate choices of a_{jj} and b_{jj} would not suffice to address this since it still leaves a solitary x_j in the numerator of the capacity term.

Beware that a representation using the above basic impact functions may not be immediately obvious, as in the left-hand sides of the following examples:

$$\prod_{i=1}^{n}(1+a_i)^{x_i} = \exp\left(\sum_{i=1}^{n}\ln(1+a_i)x_i\right);$$

$$(a_1 - a_2)^2 a_1 a_2 x_1 x_2$$
$$= (a_1 x_1 + a_2 x_2)(a_1^3 x_1 + a_2^3 x_2) - (a_1^2 x_1 + a_2^2 x_2)^2.$$

However, we expect such functions to be a rare occurrence in application.

III. BUILDING MODELS

We can use impact functions as an ansatz for constructing consistent ecosystem models tailored to a given experimental scenario. This is particularly relevant when deducing a model from assays of a huge number of populations, which become increasingly available thanks to high-throughput experiments. Such assays usually do not provide sufficient information to include all relevant agents (nutrients, toxins, etc.) into the model, thus rendering the models non-mechanistic. Moreover, in such approaches, one can rarely exclude the case of populations with nearly identical properties.

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When building a model (that does not feature higher-order interactions), it is often appropriate to assume that there is one building block of the form of Eq. 2 for each of the m experimentally determined interaction parameters. Fewer building blocks would mean unused parameters, while more building blocks would result in models that are usually overly complex. For illustration of the latter, the arguably simplest impact function that requires two building blocks of the form of Eq. 2 while featuring only one parameter is:

$$x_1, x_2, a_1, a_2 \mapsto (a_1 x_1 + a_2 x_2)(a_1^2 x_1 + a_2^2 x_2).$$

In many applications, such complexity does not level with our knowledge about the system and would thus violate Occam's razor by trying to model observations in an overly complex manner. If we have only one building block for a given parameter, we can simplify Eq. 2 to:

$$\mathbf{x}, \mathbf{a} \mapsto \zeta\left(\sum_{i=1}^{n} b_i x_i\right), \qquad \text{with} \qquad b_i := \kappa(a_i). \quad (4)$$

This is appropriate if $\mathbf{a}$ and κ are beyond the scope of the model in question, for example because they are not experimentally accessible.

A.   Example: Deducing a Model for Urinary-Tract Infections

As a demonstration of our framework, we apply it to construct a new model for the scenario of polymicrobial urinary-tract infections from Ref. 15 (see Box 1). This model shall use the same data and also employ ordinary differential equations. We have two experimental interaction parameters and therefore make an ansatz using two basic impact functions for the reasons outlined above:

$$\dot{x}_j = \mathcal{R}_j(\mathbf{x}, \mathbf{a}) := x_j \rho_j\left(\sum_{k=1}^{n} r_{jk} x_k\right) \varsigma_j\left(\sum_{k=1}^{n} s_{jk} x_k\right) \quad (5)$$

where $a_{j1} := r_j$ and $a_{j2} := s_j$.

Like the model from Ref. 15 (Eq. 1 from Box 1), we assume that a population's abundance also represents its footprint, i.e., the nutrients, toxins, and other relevant substances produced or depleted by that population. Hence featuring the death of individuals in our model could lead to implausible outcomes, as it would undo its footprint. This simplification is justified as we assume the major cause of declining populations to be dilution of the entire system, which also affects the footprint. Note that this is another limitation of the model from Ref. 15, as it allows populations to decline without dilution (see, e.g., Fig. 1). We furthermore assume that there is no lag phase caused by populations adapting to a new environment since we lack the data to quantify it.

In the situations that were experimentally investigated, this model should reproduce the observed growth rates and capacities. First, in the absence of other strains, the initial exponential growth rate of strain j should be g_j:

$$\frac{\mathrm{d}\mathcal{R}_j}{\mathrm{d}x_j}\left(\vec{0}, \mathbf{a}\right) = g_j, \quad (6)$$

where $\vec{0}$ denotes a length-n vector of zeroes (abundances are zero unless specified otherwise). Also, if all other strains are absent and strain j has reached its saturation abundance $c_j = 1$, it should not grow anymore:

$$\mathcal{R}_j\left(\vec{0}, \mathbf{a}, x_j = 1\right) = 0. \quad (7)$$

Like Ref. 15, we assume that the medium conditioned by strain k is equivalent to an ecosystem where the strain k is fixed to an abundance of v, as the footprint of strain k is the same in both situations and makes up for most of the interaction between the strains. For the medium conditioned by strain k, the initial exponential growth rate of strain j should be g_{jk}:

$$\frac{\mathrm{d}\mathcal{R}_j}{\mathrm{d}x_j}\left(\vec{0}, \mathbf{a}, x_k = v\right) = g_{jk}. \quad (8)$$

Moreover, strain j should stop growing when it reaches c_{jk}:

$$\mathcal{R}_j\left(\vec{0}, \mathbf{a}, x_j = c_{jk}, x_k = v\right) = 0. \quad (9)$$

From Eqs. 5–9, it is straightforward to derive constraints on the functions ρ_j and ς_j and to determine the parameters r_{jk} and s_{jk} in dependence of these functions, g_j, g_{jk} and c_{jk} (see Appendix D). Making simple choices for ρ_j and ς_j within these constraints and accounting for singularities and discontinuities (see Appendix D), we arrive at the following model (with $\lceil z \rceil := \max(0, z)$):

$$\dot{x}_j = x_j \left[g_j + \sum_{k=1}^{n} \frac{g_{jk} - g_j}{v} x_k\right] \cdot \left[1 - \left\lceil\sum_{k=1}^{n} \frac{1 - c_{jk}}{v} x_k\right\rceil^q\right]. \quad (10)$$

To compare this model with the previous one (Eq. 1 from Box 1), we use both to simulate the scenario of a growth experiment with regular dilution that has a known outcome (see Fig. 3). We note that quantitatively predicting experimental scenarios such as these without in-depth knowledge about the involved strains is a highly difficult challenge. Moreover, the high-throughput interaction data is restricted; for example, it does not feature higher-order interactions, and the supernatant used to determine interactions will not contain toxins whose production is triggered by products of its target. We therefore do not expect either model to have a high absolute predictive power. We assume that the abundances had converged when they were experimentally observed (see Fig. 3), and thus the experimental results are not a snapshot of an oscillatory behaviour (beyond the expected effects or a regular dilution). This is corroborated by the replicates being in good agreement and oscillations only occurring in one of the 16 simulations. We find that both models are in equally good or bad agreement with the experiment for six communities (1, 2, 4, 5, 6, and 8), while the predictions of Eq. 10 are better for two communities (3 and 7). Given the low number of samples, we refrain from further quantifying the agreements. These results indicate that models satisfying our criteria are at least equally suitable for describing ecosystem dynamics. Our results do not challenge the conclusions of Ref. 15, which
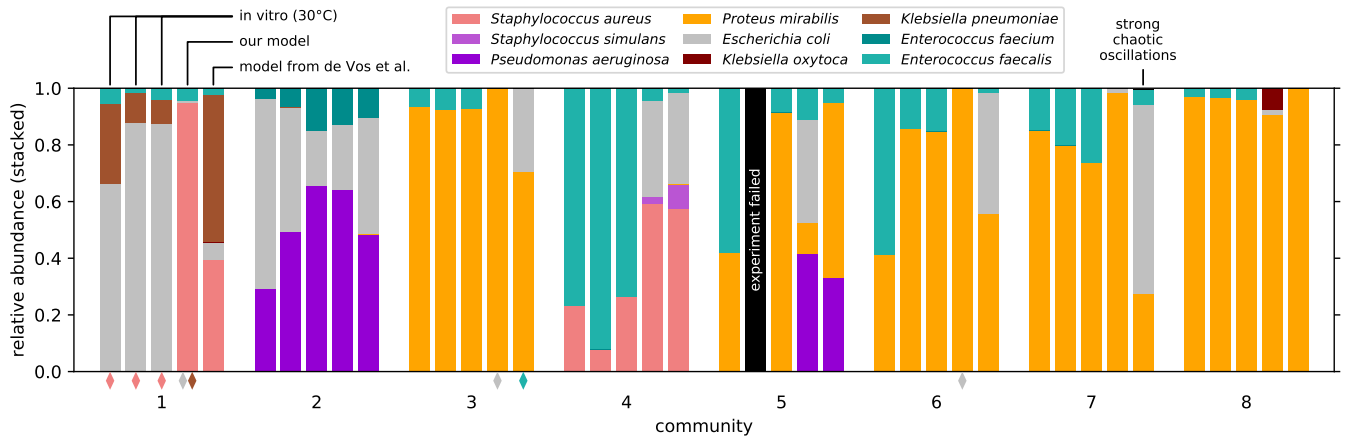
FIG. 3. Comparison of the final relative abundances of in-vitro experiments from Ref. 15 (cf. Fig. S7 B) and simulations with our model (Eq. 10) and the model from Ref. 15 (see Box 1). Communities are numbered as in Ref. 15. For the in-vitro experiments, each strain was inoculated at a fixed optical density ($OD_{600} = 0.001$) grown for $4 \times 30\,\text{h}$ and diluted by a factor of $\frac{1}{36}$ in between. Each experiment was performed in triplicate. Final abundances were determined from colony-forming units on Chromagar. The simulations mimicked the experimental procedure. Diamonds at the bottom indicate an abundance of the respective population between 10^{-3} and 10^{-2}. Community 2 featured two strains of *Enterococcus faecium*, for which we only report the summed populations since they could not be distinguished in experiment. All simulations converged, except for the model from Ref. 15 and Community 7, which exhibited strong chaotic fluctuations. See Appendix A for details of the simulation.

is expected to some extent since both models have the same fixed points if the growth term is ignored and $c_{jk} < 1 \; \forall j, k$ and thus can be expected to yield similar final states (see for example Fig. 1).

IV. DISCUSSION

While we motivated and exemplified our framework with applications to non-mechanistic models based on high-throughput data, our axioms can be required for all models that operate on the population level. We consider exceptions from this to be rare and deserving justification. For instance, if we can be sure that populations do not interbreed (i.e., contain species as defined by Mayr), replacing a population with two copies with half the abundance affects the availability of partners for sexual reproduction. Thus, the function modelling this availability must not be clone-consistent. While many popular models such as most variations of the Volterra model [4] comply with our axioms, others do not (the models from Ref. 24–27, Eqs. 3, 11, and 12 in Ref. 28, the NFR model in Ref. 29, Eq. 3 in Ref. 30, Figs. 3b and c in Ref. 2, and Eq. 1 from Box 1). However, for reasons we elaborate in the following, this does not necessarily mean that they should be dismissed outright.

In case of mechanistic models, applying our framework usually means that each mechanism is covered by its own (typically basic) impact function with many zero parameters, namely whenever the respective population is not involved in the mechanism. Taking this approach to the extreme, it is possible to extend every term to an impact function with enough assumptions. For instance, suppose a population j exclusively occupies its niche (which implies no other pop-

ulations with identical properties) and $u - x_j$ is the size of the remaining niche available to this population. Then we can extend the latter term to an impact function:

$$u - x_j = u - \sum_k a_{jk} x_k, \qquad (11)$$

where a_{jk} describes to what extent population k occupies the niche of population j and per our assumptions has the values $a_{kk} = 1$ and $a_{jk} = 0$ for $j \neq k$. Here, the value of our framework is to prompt the question: What assumptions need to be made to comply with the axioms and are these assumptions justified?

Many pure modelling studies use a model of the general form:

$$\dot{x}_j = x_j \left(g_j + \sum_{k=1}^{n} \eta_{jk}(x_k) \right),$$

where g_j is the unperturbed growth rate of population j. If all η_{jk} are linear, this kind of model employs a single basic impact function and requires no further assumption. If, on the other hand, the η_{jk} are non-linear, each of them has to correspond to one basic impact function, which requires justification that each of them only depends on one population. One assumption yielding this would be that each η_{jk} reflects one interaction mechanism which is exclusive to the impact of population k on population j. Moreover, models of the above form can either feature 1 or n impact functions (depending on whether η_{jk} is linear), but do not capture the middle ground in between. Since these basic impact functions can be roughly associated with interaction mechanisms, this limitation may be relevant beyond our framework. As an alternative filling

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this gap, our framework suggests general models of the form:

$$\dot{x}_j = x_j g_j \prod_{i=1}^{l} \eta_i \left(\sum_{k=1}^{n} a_{jki} x_k \right), \qquad (12)$$

where l is the number of impact functions. In Sec. III A we used such a model with $l = 2$ as an ansatz (g_j was incorporated in the first factor of the big product). To cover higher-order interactions, the approaches of Eqs. 3 and 12 can be combined. Amongst others, the above general model may inform studies employing random interaction parameters (e.g., Ref. 11), general modelling [31], or machine learning by narrowing down or expanding the space of possible models taken into consideration. We note that for a high l, it may make sense to regard a distribution of parameters that contains a considerable amount of zeroes, corresponding to populations not participating in some mechanism.

Finally we emphasise that our approach is general and not limited to the types of models featured in our examples: It is not restricted to models employing ordinary differential equations, but can also be applied to models with discrete time, noise, or delay. Also, higher-order interactions are covered by our framework. Moreover, while we mainly used impact functions to describe the impact of a set of populations on a population, both the targets and the source may be something else, e.g., a resource or toxin concentration or an aggregated observable such as the pH value. For example, the impact of the ecosystem on substances in the model proposed by Ref. 32 can be described in terms of impact functions. We particularly note the parallels to two pharmacological approaches to describe the cumulative effect of two drugs that are not synergistic or antagonistic, i.e., are not subject to higher-order interactions [33, 34]:

- Loewe additivity, which is based on arguments similar to clone consistency (I4) and holds if the two drugs affect the same component of the cell,

- Bliss independence, which violates clone consistency (I4) at first glance and holds if the two drugs affect different components of the cell.

In our framework, drugs that target the same cell component would correspond to using the same interaction mechanism and thus would be captured by the same basic impact function. The effect of a complex drug cocktail could be captured by several Bliss-independent basic impact functions, each of which comprises a series of Loewe-additive components.

V. CONCLUSION

We introduced impact functions, which are basic building blocks of ecosystem models adhering to axioms capturing fundamental consistency requirements. We mathematically proved that such impact functions must have linear combinations of parameters and abundances at their core. We demonstrated that impact functions can be used to easily build models complying with the axioms to capture a specific experimental scenario – though one should still beware that the

model makes sense in respects not covered by the axioms. Our framework also informs the form of more general models, pointing out potential new directions of research in this area or outlining the space of possible models. Conversely, the absence of impact functions in a model points out that it makes implicit assumptions or has consistency problems. We are therefore confident that our framework can form a backbone for a wide range of ecological modelling studies.

Appendix A: Simulation Details

For simulations with both, the model from Ref. 15 (Eq. 1 from Box 1) and our model described by Eq. 10, we use the data from Ref. 15 as is, with the exception of data describing interactions between two identical strains: First, in the experiment, a strain cannot grow on the portion of the medium that is its own supernatant, but only on the portion that is fresh medium, which makes up $1 - v = 0.6$ of the medium. We set $c_{ii} = 1 - v$ to adhere to this ideal. Second, in the medium conditioned by itself, a strain's growth rate should at best slightly lower than in an unconditioned medium and at worst be proportional to the concentration of nutrients, and thus to $1 - v$. We therefore restrict g_{ii} to the interval $[(1 - v)g_i, (1 - \epsilon)g_i]$ with $\epsilon = 0.01$. Without these adjustments, we would obtain implausible results, e.g., in case of $c_{ii} > 1 - v$, the respective strain could never stop growing since it effectively increases the size of its own niche.

We performed all simulations with JiTCODE [35] using the DoPri5 method. To obtain continuity as required by the integration method, we approximate $\lceil z \rceil = \max(0, z) \approx \frac{1}{2}\left(z + \sqrt{z^2 + \epsilon^2}\right)$ with $\epsilon = 0.001$.

We converted abundances in the simulation results to optical densities by undoing the respective normalisation of abundances (fixing $c_j = 1$ in Box 1). We then converted the optical densities to displayed abundances (in Figs. 1 and 3) by approximating that optical density is proportional to biovolume.

Appendix B: Arithmetic Example for Inconsistencies in a Model

We here provide an arithmetic example for an inconsistent behaviour of the model described by Eq. 1 from Box 1. This example features no growth interaction and thus does not rely on how we chose identical populations to affect each other's

growth (see Appendix A) – a choice that is not clear without experiment.

We consider the case of three populations $\{1, 2, 3\} =: J$ with the first two populations having identical properties. We choose $g_j = 1 \,\forall j \in J, a_{j,k} = 0 \,\forall j, k \in J \times J$, i.e., the growth term is not affected by interaction and is always 1. Finally, we let the coefficients of the capacity term be:

$$b = \begin{pmatrix} \cdot & -1 & \frac{1}{4} \\ -1 & \cdot & \frac{1}{4} \\ \frac{1}{4} & \frac{1}{4} & \cdot \end{pmatrix}.$$

$b_{12} = -1$ and $b_{21} = -1$ reflects that two populations with identical properties deplete each other's niches. Now, consider two states of the ecosystem $x = \left(\frac{1}{4}, \frac{1}{4}, 1 \right)$ and $\hat{x} = \left(\frac{1}{2}, 0, 1 \right)$. As the first two populations are indistinguishable, these states describe an equivalent situation. Thus, they should also evolve equivalently, i.e., the temporal derivative of the summed populations 1 and 2 should be the same in both cases: $\dot{x}_1 + \dot{x}_2 = \dot{\hat{x}}_1 + \dot{\hat{x}}_2 = \dot{\hat{x}}_1$. However,

$$\dot{x}_1 + \dot{x}_2 = 2\dot{x}_1 = 2\frac{1}{4}\left(1 - \frac{\frac{1}{4}}{\lceil 1 - \frac{1}{4} + \frac{1}{4}\rceil}\right) = \frac{3}{8}$$

$$\neq \dot{\hat{x}}_1 = \frac{1}{2}\left(1 - \frac{\frac{1}{2}}{\lceil 1 + 0 + \frac{1}{4}\rceil}\right) = \frac{1}{2}\left(1 - \frac{4}{10}\right) = \frac{3}{10}.$$

Appendix C: Mathematical proofs

To prove Lemma 1 as stated in Box 1, we first prove two other lemmas:

Lemma 2. *Suppose* $\mathbf{x}, \hat{\mathbf{x}} \in X$ *and* $\mathbf{a}, \hat{\mathbf{a}} \in A$ *are such that:*

$$\sum_{i=1}^{n} a_i^j x_i = \sum_{i=1}^{n} \hat{a}_i^j \hat{x}_i \quad \forall j \in \{1, \ldots\}. \qquad (C1)$$

Let $\mathfrak{a}_1 > \mathfrak{a}_2 > \ldots > \mathfrak{a}_s >= 0$ *be the sequence of ordered absolute non-zero values of* a_i *and* $\hat{a}_i$ *for all* $i \in 1, \ldots, n$. *For each* $p \in 1, \ldots, s$ *let* $E_p^+, E_p^-, \hat{E}_p^+,$ *and* $\hat{E}_p^-$ *be the maximal sets of indices for which the absolute value of* $\mathfrak{a}_p$ *is assumed, more specifically:*

$$\begin{aligned} a_k = \mathfrak{a}_p \,\forall k \in E_p^+, \qquad a_k = -\mathfrak{a}_p \,\forall k \in E_p^-, \\ \hat{a}_k = \mathfrak{a}_p \,\forall k \in \hat{E}_p^+, \qquad \hat{a}_k = -\mathfrak{a}_p \,\forall k \in \hat{E}_p^-. \end{aligned} \qquad (C2)$$

We denote $E_p := E_p^+ \cup E_p^-$ *and* $\hat{E}_p := \hat{E}_p^+ \cup \hat{E}_p^-$. *Then:*

$$z_p^+ := \sum_{i \in E_p^+} x_i = \sum_{i \in \hat{E}_p^+} \hat{x}_i =: \hat{z}_p^+ \quad \forall p \in \{1, \ldots, s\},$$

$$z_p^- := \sum_{i \in E_p^-} x_i = \sum_{i \in \hat{E}_p^-} \hat{x}_i =: \hat{z}_p^- \quad \forall p \in \{1, \ldots, s\}. \qquad (C3)$$

We show Eq. C3 by induction over p. We first note that the lemma trivially holds for all $p \in \{\}$. In the following we

show that, if lemma holds for all $p \in \{1, \ldots, r-1\}$ with $r \in \{0, \ldots, s\}$, it also holds for all $p \in \{1, \ldots, r\}$. To this end, we show that the linear combinations must also be equal when only considering coefficients with absolute value $\mathfrak{a}_{r+1}$ or lower (for all j):

$$\sum_{p=r}^{s} \sum_{i \in E_p} a_i^j x_i = \sum_{p=1}^{s} \sum_{i \in E_p} a_i^j x_i - \sum_{p=1}^{r-1} \sum_{i \in E_p} a_i^j x_i$$

$$\stackrel{C2}{=} \sum_{i=1}^{n} a_i^j x_i - \sum_{p=1}^{r-1} \left(\mathfrak{a}_p^j \sum_{i \in E_p^+} x_i + (-\mathfrak{a}_p)^j \sum_{i \in \hat{E}_p} x_i \right)$$

$$\stackrel{C1,C3}{=} \sum_{i=1}^{n} \hat{a}_i^j \hat{x}_i - \sum_{p=1}^{r-1} \left(\mathfrak{a}_p^j \sum_{i \in \hat{E}_p^+} \hat{x}_i + (-\mathfrak{a}_p)^j \sum_{i \in \hat{E}_p} \hat{x}_i \right)$$

$$\stackrel{C2}{=} \sum_{p=1}^{s} \sum_{i \in \hat{E}_p} \hat{a}_i^j \hat{x}_i - \sum_{p=1}^{r-1} \sum_{i \in \hat{E}_p} \hat{a}_i^j \hat{x}_i = \sum_{p=r}^{s} \sum_{i \in \hat{E}_p} \hat{a}_i^j \hat{x}_i \qquad (C4)$$

If $z_p^+ + z_p^- \neq 0$ and $\hat{z}_p^+ + \hat{z}_p^- \neq 0$ the above equality will be dominated by $\mathfrak{a}_r^j$ for $j \to \infty$, which gives us:

$$1 \stackrel{C4}{=} \lim_{\substack{j \to \infty \\ j \text{ even}}} \frac{\sum_{p=r}^{s} \sum_{i \in E_p} a_i^j x_i}{\sum_{p=r}^{s} \sum_{i \in \hat{E}_p} \hat{a}_i^j \hat{x}_i} = \lim_{\substack{j \to \infty \\ j \text{ even}}} \frac{\sum_{i \in E_r} a_i^j x_i}{\sum_{i \in \hat{E}_r} \hat{a}_i^j \hat{x}_i}$$

$$\stackrel{C2}{=} \lim_{\substack{j \to \infty \\ j \text{ even}}} \frac{\sum_{i \in E_r} \mathfrak{a}_r^j x_i}{\sum_{i \in \hat{E}_r} \mathfrak{a}_r^j \hat{x}_i} = \frac{\sum_{i \in E_r} x_i}{\sum_{i \in \hat{E}_r} \hat{x}_i} \stackrel{C3}{=} \frac{z_p^+ + z_p^-}{\hat{z}_p^+ + \hat{z}_p^-}$$

$$\implies z_p^+ + z_p^- = \hat{z}_p^+ + \hat{z}_p^- \qquad (C5)$$

In case that exactly one of $z_p^+ + z_p^-$ and $\hat{z}_p^+ + \hat{z}_p^-$ is zero, the above yields a contradiction due to the limit evaluating as either 0 or ∞, and hence this cannot be the case. If both are zero, the concluded equation holds without further ado. Analogously, we obtain:

$$1 \stackrel{C4}{=} \lim_{\substack{j \to \infty \\ j \text{ odd}}} \frac{\sum_{p=r}^{s} \sum_{i \in E_p} a_i^j x_i}{\sum_{p=r}^{s} \sum_{i \in \hat{E}_p} \hat{a}_i^j \hat{x}_i} = \lim_{\substack{j \to \infty \\ j \text{ odd}}} \frac{\sum_{i \in E_r} a_i^j x_i}{\sum_{i \in \hat{E}_r} \hat{a}_i^j \hat{x}_i}$$

$$\stackrel{C2}{=} \lim_{\substack{j \to \infty \\ j \text{ odd}}} \frac{\sum_{i \in E_r^+} \mathfrak{a}_r^j x_i + \sum_{i \in E_r^-} (-\mathfrak{a})_r^j x_i}{\sum_{i \in \hat{E}_r^+} \mathfrak{a}_r^j \hat{x}_i + \sum_{i \in \hat{E}_r^-} (-\mathfrak{a})_r^j \hat{x}_i}$$

$$= \frac{\sum_{i \in E_r^+} x_i - \sum_{i \in E_r^-} x_i}{\sum_{i \in \hat{E}_r^+} \hat{x}_i - \sum_{i \in \hat{E}_r^-} \hat{x}_i} \stackrel{C3}{=} \frac{z_p^+ - z_p^-}{\hat{z}_p^+ - \hat{z}_p^-}$$

$$\implies z_p^+ - z_p^- = \hat{z}_p^+ - \hat{z}_p^- \qquad (C6)$$

By adding and subtracting Eqs. C5 and C6, respectively, we arrive at $z_p^+ = \hat{z}_p^+$ and $z_p^- = \hat{z}_p^-$. $\qquad \square$

Lemma 3. *Denote* $\mathbf{x}$, $\mathbf{a}$, $\mathfrak{a}_p$, s, E_p^+, E_p^-, z_p^+, *and* z_p^- *as in Lemma 2. Let:*

$$\{q_1^+, \ldots, q_{w^+}^+\} := \{p \in \{1, \ldots, s\} \mid z_p^+ \neq 0\},$$
$$\{q_1^-, \ldots, q_{w^-}^-\} := \{p \in \{1, \ldots, s\} \mid z_p^- \neq 0\},$$

such that $\mathfrak{a}_{q_i^+} > \mathfrak{a}_{q_j^+}$ *and* $\mathfrak{a}_{q_i^-} > \mathfrak{a}_{q_j^-}$ *if* $i < j$. *Define:*

$$\tilde{\mathbf{x}} = \left(z_{q_1^+}^+, \ldots, z_{q_{w^+}^+}^+, \quad z_{q_1^-}^-, \ldots, \quad z_{q_{w^-}^-}^-, 0, \ldots, 0\right),$$
$$\tilde{\mathbf{a}} = \left(\mathfrak{a}_{q_1^+}, \ldots, \mathfrak{a}_{q_{w^+}^+}, -\mathfrak{a}_{q_1^-}, \ldots, -\mathfrak{a}_{q_{w^-}^-}, 0, \ldots, 0\right),$$

where the number of zeros at the end is $n - w^+ - w^-$. *Let* ϕ *be an impact function. Then* $\phi(\mathbf{x}, \mathbf{a}) = \phi(\tilde{\mathbf{x}}, \tilde{\mathbf{a}})$.

We show this by transforming blocks of arguments to the target form (with some zero arguments added if necessary) using the impact-function axioms, and finally reorder the indices (populations) using Axiom I1.

The first kind of block we consider are blocks of equal positive parameters (a_i), i.e., E_i^+ for some i. Let $\{e_1, \ldots, e_v\} := E_{q_i^+}^+$. Then for some $\check{\mathbf{x}}$, $\check{\mathbf{a}}$:

$$\phi\Big(\check{\mathbf{x}}, \mathsf{x}_{e_1} = x_{e_1} \ , \ \mathsf{x}_{e_2} = x_{e_2}, \ \ldots, \ \mathsf{x}_{e_v} = x_{e_v},$$
$$\check{\mathbf{a}}, \ \mathsf{a}_{e_1} = \mathfrak{a}_{q_i^+} \ , \ \mathsf{a}_{e_2} = \mathfrak{a}_{q_i^+}, \ \ldots, \ \mathsf{a}_{e_v} = \mathfrak{a}_{q_i^+} \Big)$$
$$\overset{\text{I4}}{=} \phi\Big(\check{\mathbf{x}}, \ \mathsf{x}_{e_1} = \sum_{i \in E_{q_i^+}^+} x_i, \ \mathsf{x}_{e_2} = 0 \ , \ \ldots, \ \mathsf{x}_{e_v} = 0,$$
$$\check{\mathbf{a}}, \ \mathsf{a}_{e_1} = \mathfrak{a}_{q_i^+} \ , \ \mathsf{a}_{e_2} = \mathfrak{a}_{q_i^+}, \ \ldots, \ \mathsf{a}_{e_v} = \mathfrak{a}_{q_i^+} \Big)$$
$$\overset{\text{C3}}{=} \phi\Big(\check{\mathbf{x}}, \ \mathsf{x}_{e_1} = z_{q_i^+}^+ \ , \ \mathsf{x}_{e_2} = 0 \ , \ \ldots, \ \mathsf{x}_{e_v} = 0,$$
$$\check{\mathbf{a}}, \ \mathsf{a}_{e_1} = \mathfrak{a}_{q_i^+} \ , \ \mathsf{a}_{e_2} = \mathfrak{a}_{q_i^+}, \ \ldots, \ \mathsf{a}_{e_v} = \mathfrak{a}_{q_i^+} \Big)$$
$$\overset{\text{I2}}{=} \phi\Big(\check{\mathbf{x}}, \ \mathsf{x}_{e_1} = z_{q_i^+}^+ \ , \ \mathsf{x}_{e_2} = 0 \ , \ \ldots, \ \mathsf{x}_{e_v} = 0,$$
$$\check{\mathbf{a}}, \ \mathsf{a}_{e_1} = \mathfrak{a}_{q_i^+} \ , \ \mathsf{a}_{e_2} = 0 \ , \ \ldots, \ \mathsf{a}_{e_v} = 0 \ \Big).$$

Blocks of equal negative parameters (E_i^-) can be transformed analogously.

If a parameter a_i is zero, we transform the single-index block $\{i\}$ to zero (for some $\check{\mathbf{x}}$, $\check{\mathbf{a}}$):

$$\phi(\check{\mathbf{x}}, \check{\mathbf{a}}, \mathsf{x}_i = \tilde{x}_i, \mathsf{a}_i = 0) \overset{\text{I3}}{=} \phi(\check{\mathbf{x}}, \check{\mathbf{a}}, \mathsf{x}_i = 0, \mathsf{a}_i = 0).$$

Finally, if an abundance x_i is zero, we transform the single-index block $\{i\}$ to zero (for some $\check{\mathbf{x}}$, $\check{\mathbf{a}}$):

$$\phi(\check{\mathbf{x}}, \check{\mathbf{a}}, \mathsf{x}_i = 0, \mathsf{a}_i = \check{a}_i) \overset{\text{I2}}{=} \phi(\check{\mathbf{x}}, \check{\mathbf{a}}, \mathsf{x}_i = 0, \mathsf{a}_i = 0). \quad \square$$

Lemma 1. *Suppose* $\mathbf{x}, \hat{\mathbf{x}} \in X$ *and* $\mathbf{a}, \hat{\mathbf{a}} \in A$ *are such that:*

$$\sum_{i=1}^{n} a_i^j x_i = \sum_{i=1}^{n} \hat{a}_i^j \hat{x}_i \quad \forall j \in \{1, \ldots\}.$$

Let ϕ *be an impact function. Then* $\phi(\mathbf{x}, \mathbf{a}) = \phi(\hat{\mathbf{x}}, \hat{\mathbf{a}})$.

To prove this, we only need to note how the transformed arguments $\tilde{\mathbf{x}}$ and $\tilde{\mathbf{a}}$ only depend on the parameters values a_i corresponding to non-zero total abundance z_i^+ and z_i^t. Those in turn are equal per Lemma 2. Thus:

$$\phi(\mathbf{x}, \mathbf{a}) \overset{\text{L. 3}}{=} \phi(\tilde{\mathbf{x}}, \tilde{\mathbf{a}}) \overset{\text{L. 2}}{=} \phi\left(\hat{\tilde{\mathbf{x}}}, \hat{\tilde{\mathbf{a}}}\right) \overset{\text{L. 3}}{=} \phi(\hat{\mathbf{x}}, \hat{\mathbf{a}}). \quad \square$$

Appendix D: Deriving a New Model for UTI strains – the Legwork

Expanding Eq. 7, we obtain: $0 = \mathcal{R}_j\left(\vec{0}, \mathbf{a}, \mathsf{x}_j = 1\right) = \rho_j(r_{jj})\varsigma_j(s_{jj})$. Assuming that the two factors do not "take turns" in being zero for different j, this means that either $\rho_j(r_{jj}) = 0$ or $\varsigma_j(s_{jj}) = 0$. Without loss of generality, we assume that the latter applies, thus assigning ς_j the role of quantifying the carrying capacity. Furthermore, we choose $s_{jj} = 1$ and $\varsigma_j(0) = 1$. These are normalisation choices, as they can be compensated by including a respective factor in ς_j or ρ_j respectively. Using this and expanding Eq. 9, we obtain:

$$0 = \mathcal{R}_j\left(\vec{0}, \mathbf{a}, \mathsf{x}_j = c_{jk}, \mathsf{x}_k = v\right)$$
$$= c_{jk} \rho_j(r_{jj} c_{jk} + r_{jk} v) \varsigma_j(c_{jk} + s_{jk} v).$$

Assuming that ς_j is again responsible for the product being zero and it has only one root, namely 1, we arrive at: $c_{jk} + s_{jk} v = 1$, and thus: $s_{jk} = \frac{1 - c_{jk}}{v}$. Note that since $s_{jj} = 1$, this is consistent with our choice of $c_{jj} = 1 - v$ (see Appendix A).

Using the above, we can expand Eqs. 6 and 8:

$$g_j = \frac{\mathrm{d}\mathcal{R}_j}{\mathrm{d}x_j}\left(\vec{0}, \mathbf{a}\right) = \rho_j(0)\varsigma_j(0), = \rho_j(0), \tag{D1}$$

$$g_{jk} = \frac{\mathrm{d}\mathcal{R}_j}{\mathrm{d}x_j}\left(\vec{0}, \mathbf{a}, \mathsf{x}_k = v\right) = \rho(vr_{jk})\varsigma(vs_{jk})$$
$$\Longrightarrow \rho(vr_{jk}) = \frac{g_{jk}}{\varsigma(vs_{jk})} = \frac{g_{jk}}{\varsigma(1 - c_{jk})}. \tag{D2}$$

We choose the arguably simplest function to fulfil the criteria for ρ, namely $\rho_j(z) := g_j + z$. This has the consequence:

$$\rho_{jk} = \frac{1}{v}\left(\frac{g_{jk}}{\varsigma(1 - c_{jk})} - g_j\right). \tag{D3}$$

A group of functions fulfilling the criteria for ς is: $\varsigma_j(z) := 1 - \lceil z \rceil^q$ with $q > 0$ and $\lceil z \rceil := \max(0, z)$. Here, the free parameter q controls how early and smoothly the saturation effect of a depleted niche kicks in. Note that this choice results in terms similar to what Ref. 36 named *hyperlogistic*.

Finally, like Ref. 15, we constrain the growth and capacity term to be non-negative. Putting everything together, we arrive at the model:

$$\dot{x}_j = x_j \left[g_j + \sum_{k=1}^{n} \frac{1}{v}\left(\frac{g_{jk}}{1 - \lceil 1 - c_{jk}\rceil^q} - g_j\right)x_k\right]$$
$$\cdot \left[1 - \left\lceil \sum_{k=1}^{n} \frac{1 - c_{jk}}{v} x_k\right\rceil^q\right]. \tag{D4}$$

A problem with this model is that for $0 < x_k < 1$, we have: $\lim_{c_{jk} \to 0} \dot{x}_j = \lim_{c_{jk} \to 0} \mathcal{R}_j(\mathbf{x}, \mathbf{a}) = \infty$. Now, $c_{jk} = 0$ means that there is no growth of strain j in the medium conditioned by strain k and thus we already have a problem with experimentally determining g_{jk}. Thus, one might argue that the actual point of the singularity requires a dedicated case distinction anyway. However, $\lim_{c_{jk} \to 0} \dot{x}_j = \infty$. also means that $\dot{x}_j$ becomes arbitrarily large for small c_{jk}. A way to address this problem is to consider the case $q \to \infty$, or more specifically:

$$\lceil \varsigma_j(z) \rceil = \begin{cases} 1 & \text{if } z < 1 \\ 0 & \text{if } z \geq 1 \end{cases}$$

In this case, the term $\varsigma(1 - c_{jk})$ in Eq. D2 can be assumed to be 1 (otherwise, we would have the aforementioned problem of not being able to experimentally determine g_{jk}). This eliminates the singularity, but also renders the model not continuously differentiable.

In our simulations, we therefore make a trade-off between complying with Eq. 8 and the numerical benefits of a continuously differentiable model by setting $q = 10$ and approximating $\varsigma(1 - c_{jk}) \approx \lim_{p \to \infty} \varsigma(1 - c_{jk}) = 1$ in Eq. D2, thus arriving at:

$$\dot{x}_j = x_j \left[g_j + \sum_{k=1}^{n} \frac{g_{jk} - g_j}{v} x_k \right] \cdot \left[1 - \left[\sum_{k=1}^{n} \frac{1 - c_{jk}}{v} x_k \right]^{10} \right].$$
$$\text{(D5)}$$

[1] U. Bastolla, M. Lässig, S. C. Manrubia, and A. Valleriani, J. Theor. Bio. **235**, 521 (2005).
[2] D. Gonze, K. Z. Coyte, L. Lahti, and K. Faust, Curr. Opin. Microbiol. **44**, 41 (2018).
[3] F. S. Valdovinos, Ecol. Lett. (2019), 10.1111/ele.13279.
[4] V. Volterra, ICES J. Mar. Sci. **3**, 3 (1928).
[5] J. M. Levine, J. Bascompte, P. B. Adler, and S. Allesina, Nature **546**, 56 (2017).
[6] J. C. D. Terry, R. J. Morris, and M. B. Bonsall, Ecol. Lett. **20**, 1219 (2017).
[7] R. M. May, Nature **238**, 413 (1972).
[8] D. T. Haydon, Ecology **81**, 2631 (2000).
[9] S. Allesina and S. Tang, Popul. Ecol. **57**, 63 (2015).
[10] K. Z. Coyte, J. Schluter, and K. R. Foster, Science **350**, 663 (2015).
[11] E. Bairey, E. D. Kelsic, and R. Kishony, Nat. Comm. **7**, 12285 (2016).
[12] J. Grilli, G. Barabás, M. J. Michalska-Smith, and S. Allesina, Nature **548**, 210 (2017).
[13] J. H. Vandermeer, Ecology **50**, 362 (1969).
[14] E. D. Kelsic, J. Zhao, K. Vetsigian, and R. Kishony, Nature **521**, 516 (2015).
[15] M. G. J. de Vos, M. Zagorski, A. McNally, and T. Bollenbach, Proc. Natl. Acad. Sci. U.S.A. **114**, 10666 (2017).
[16] M. M. Mayfield and D. B. Stouffer, Nat. Ecol. Evol. **1**, 0062 (2017).
[17] R. A. Long and F. Azam, Appl. Environ. Microbiol. **67**, 4975 (2001).
[18] K. Vetsigian, R. Jajoo, and R. Kishony, PLOS Biol. **9**, 1 (2011).
[19] O. X. Cordero, H. Wildschutte, B. Kirkup, S. Proehl, L. Ngo, F. Hussain, F. Le Roux, T. Mincer, and M. F. Polz, Science **337**, 1228 (2012).
[20] J. Kehe, A. Kulesa, A. Ortiz, C. M. Ackerman, S. G. Thakku, D. Sellers, S. Kuehn, J. Gore, J. Friedman, and P. C. Blainey,

Proc. Natl. Acad. Sci. U.S.A. **116**, 12804 (2019).
[21] S. Widder, R. J. Allen, T. Pfeiffer, T. P. Curtis, C. Wiuf, W. T. Sloan, O. X. Cordero, S. P. Brown, B. Momeni, W. Shou, H. Kettle, H. J. Flint, A. F. Haas, B. Laroche, J.-U. Kreft, P. B. Rainey, S. Freilich, S. Schuster, K. Milferstedt, J. R. van der Meer, T. Großkopf, J. Huisman, A. Free, C. Picioreanu, C. Quince, I. Klapper, S. Labarthe, B. F. Smets, H. Wang, Isaac Newton Institute Fellows, and O. S. Soyer, ISME J. **10**, 2557 (2016).
[22] E. Bishop, Pac. J. Math. **11**, 777 (1961).
[23] T. J. Ransford, Math. Proc. Camb. Phil. Soc. **96**, 309–311 (1984).
[24] E. L. Coutlee and R. I. Jennrich, Am. Nat. **102**, 307 (1968).
[25] S. Marino, N. T. Baxter, G. B. Huffnagle, J. F. Petrosino, and P. D. Schloss, Proc. Natl. Acad. Sci. U.S.A. **111**, 439 (2014).
[26] J. J. Qian and E. Akçay, BioRxiv (2019), 10.1101/643478.
[27] E. Thébault and C. Fontaine, Science **329**, 853 (2010).
[28] S. Uchida, B. Drossel, and U. Brose, Ecol. Model. **206**, 263 (2007).
[29] F. S. Valdovinos, P. Moisset de Espanés, J. D. Flores, and R. Ramos-Jiliberto, Oikos **122**, 907 (2013).
[30] B. Momeni, L. Xie, and W. Shou, eLife **6** (2017), 10.7554/eLife.25051.
[31] T. Gross, L. Rudolf, S. A. Levin, and U. Dieckmann, Science **325**, 747 (2009).
[32] L. Niehaus, I. Boland, M. Liu, K. Chen, D. Fu, C. Henckel, K. Chaung, S. E. Miranda, S. Dyckman, M. Crum, S. Dedrick, W. Shou, and B. Momeni, Nature Comm. **10**, 2052 (2019).
[33] W. Greco, H.-D. Unkelbach, G. Pöch, J. Sühnel, M. Kundi, and W. Bödeker, Arch. Complex Environ. Stud. **4**, 65 (1992).
[34] D. Y. Baeder, G. Yu, N. Hozé, J. Rolff, and R. R. Regoes, Phil. T. R. Soc. B **371**, 20150294 (2016).
[35] G. Ansmann, Chaos **28**, 043116 (2018).
[36] M. E. Turner, E. L. Bradley, K. A. Kirk, and K. M. Pruitt, Math. Biosci. **29**, 367 (1976).