Understanding the variability of pairwise coexistence within multispecies systems

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Abstract

The persistence of virtually every single species depends on both the presence of other species and the heterogeneous environmental conditions. Because in natural settings many of these conditions are unknown, research has been centered on finding the fraction of possible conditions (probability) leading to species coexistence. The focus has been on the coexistence probability of two species in isolation or that of an entire multispecies system. However, it is unclear how a system can affect differently the coexistence expectation of each of its constituent pairs. Here, we derive long-term (using analytical calculations) and short-term (using simulations and experimental data) system-level indicators of the effect of multispecies systems on pairwise coexistence under unknown environmental conditions. We demonstrate that the fraction of conditions incompatible with the possible coexistence of a pair of species in isolation tends to become vanishingly small within systems of increasing numbers of species. Yet, the fraction of conditions allowing pairwise coexistence in isolation remains approximately the center of the probability distribution of pairwise coexistence across all possible systems. While the likelihood of short-term survival is always greater than or equal to that of long-term survival, we found in general stronger (resp. weaker) short-term buffering effects within systems than in isolation under negative (resp. positive) long-term effects. We show that both long-term and short-term effects of a system are not equally distributed across all of its possible pairs, but these differences can be mapped and anticipated under environmental uncertainty.

Author Summary

It is debated whether the frequency at which two species coexist in isolation or within a single environmental context is representative of their coexistence expectation within larger systems and across different environmental conditions. Here, using analytical calculations, simulations, and experimental data, we show how multispecies systems can provide the opportunity of pairwise coexistence regardless of whether a pair of species cannot coexist in isolation across different environmental conditions. However, we show that this opportunity is not homogeneously granted across all pairs within the same system. We provide a framework to understand and map the long-term and short-term effects that a system has on the coexistence of each of its constituent pairs. Our work can have useful applications in bio-restoration and bio-medicine subject to unknown environmental conditions.

Introduction

The persistence of virtually all living organisms on Earth depends to a greater or lesser extent on the presence of other living organisms and on the environmental (abiotic and biotic) conditions present in a given place and time (1, 2). This observation has established a rich research program in quantifying pairwise interactions and their impact on pairwise coexistence across environmental gradients (3–8). In this line, empirical work has been focused on finding the frequency of occurrence of multiple pairs of species across different environments either in isolation or within different systems of multiple species (9–16). For example, studies have long debated whether there exists in nature pairs of species whose niches forbid their coexistence regardless of the environment—known as the checkerboard hypothesis (11, 17). Instead, experimental studies have shown that pairwise coexistence strongly depends on the details of both the system and the environment (10, 12, 18, 19). In fact, it has been shown that coexistence expectations that may operate under controlled conditions (or homogeneous environments) (12, 14) do not necessarily operate under unknown conditions (or heterogeneous environments) (5, 20). These empirical results have shown that in order to implement successful interventions in ecological systems (e.g., protection or restoration), it is essential to develop testable theory to be able to explain how emergent processes at the system level can affect the possibility that a given pair of species will coexist under different environments.

Because the environmental conditions acting on species are typically unknown and heterogeneous in natural settings, the majority of theoretical work has been centered on deriving the fraction of conditions (set of parameter values) leading to pairwise coexistence in isolation or those defining the coexistence of multiple species (8, 21–23). However, species are seldom in isolation and the coexistence of a specific combination of multiple species is expected to be rare in a random environment (5, 24, 25). Moreover, it has been demonstrated that conclusions derived from two-dimensional systems cannot always be translated into conclusions within multi-dimensional systems (26–29). Thus, it is unclear the extent to which a system can affect differently the coexistence expectation of its different pairs.

Ecological research has suggested that species embedded into multispecies systems (more than two species) may experience higher-order effects, i.e., the effect of species i on the per capita growth rate of species j might itself depend on the abundance of a third species k due to either compensatory effects, supra-additivity, trait-mediated effects, functional effects, meta-community effects, or indirect effects (8, 30–33). Unfortunately, additional research has show that it is virtually impossible to derive those potential effects since many parameter combinations can equally explain the observed ecological dynamics—a problem known as structural identifiability (34, 35). In fact, many of the interactions measured under multispecies systems are not direct effects, as studies often believe (15, 16), but chains of direct effects (36, 37). Moreover, measurements of species interactions are expected to change as a function of the type of data (i.e., snapshot or time), experiment (e.g., long term or short term), perturbations (e.g., pulse or press), and dimensionality, leading to inconsistencies and inference issues (34, 38, 39). Thus, it is unclear whether the frequency with which two species coexist in isolation is

representative of their coexistence expectation within larger systems and across different environments.

Here, we follow a geometric and probabilistic analysis based on nonlinear dynamics at equilibrium to estimate the effect of a multispecies system on pairwise coexistence under unknown environmental conditions using minimum information from pairwise species interactions. We estimate these system-level effects over the long-term (using analytical calculations) and over the short-term (using simulations and available experimental data on gut microbiota). Building on generalized Lotka-Volterra (gLV) dynamics (8), we provide a geometric understanding regarding whether the conditions limiting the coexistence of a pair of species in isolation (the known species pool consists only of this pair) remain within multispecies systems (when the known species pool increases). Next, we derive a system-level indicator of the extent to which a multispecies system can affect the probability of coexistence of a pair relative to its probability in isolation. Then, we compare the numerical and experimental effects to the analytical expectation in order to distinguish the role that multispecies systems play in shaping pairwise coexistence under short-term and long-term behavior, respectively. Finally, we show how our theory can be used to provide a cartographic representation (40) of the different long-term and short-term effects acting on each pair within a multispecies system under environmental uncertainty.

Theoretical framework

Traditional indicators of pairwise coexistence

Our theoretical framework is based on the tractability of the gLV dynamics (35), where the per-capita growth rate of species $i \in \{1, \cdots, |\mathcal{S}|\} \equiv \mathcal{S}$ is written as $f_i(\mathbf{N}; \boldsymbol{\theta}) = \theta_i - \sum_{j \in \mathcal{S}} a_{ij} N_j$, where the vector $\mathbf{N} = (N_1, \ldots, N_{|\mathcal{S}|})^\intercal$ represents the density of all species in the system $\mathcal{S}$. The matrix $\mathbf{A} = (a_{ij}) \in \mathbb{R}^{|\mathcal{S}| \times |\mathcal{S}|}$ corresponds to the interaction matrix dictating the internal structure of the system, i.e., the per-capita effect of species j on an individual of species i. The effective parameters $\boldsymbol{\theta} = (\theta_1, \ldots, \theta_{|\mathcal{S}|})^\intercal \in \mathbb{R}^{|\mathcal{S}|}$ consist of the phenomenological effect of the internal (e.g., intrinsic growth rate), abiotic (e.g., temperature, pH, nutrients), and biotic factors (e.g., unknown species, higher-order interactions) acting on the per-capita growth rate of each particular species. That is, we consider that the *effective growth rate* $\boldsymbol{\theta}$ represents the total additional effect of all the unknown potential factors as a function of the environmental conditions acting on each species independently. Note that pairwise effects a_{ij} from a given pool of species are assumed to be known.

Under steady-state dynamics (i.e., $\boldsymbol{f} = 0$), the necessary condition for species coexistence is the existence of a feasible equilibrium (i.e., $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{\theta} > 0$) (22). The combinations of the effective growth rate $\boldsymbol{\theta}$ compatible with the feasibility of a multispecies system $\mathcal{S}$ (known as the feasibility region D_F) can be described as:

$$D_F(\mathcal{S}) = \left\{ \sum_{j \in \mathcal{S}} N_j^* \mathbf{a}_j : \mathbf{A} = [\mathbf{a}_1 \ \mathbf{a}_2 \ \cdots \ \mathbf{a}_{|\mathcal{S}|}], N_j^* \in \mathbb{R}_{>0} \right\} \in \mathbb{R}^{|\mathcal{S}|},$$

where $\mathbf{a}_j$ is the jth column vector of the interaction matrix $\mathbf{A}$. Additionally, assuming no a priori information about how the environmental conditions affect the effective growth rate (41), the feasibility domain can be normalized by the volume of the entire parameter space (25) as

$$F(\mathcal{S}) = \frac{\text{vol}(D_F(\mathcal{S}) \cap \Theta^{|\mathcal{S}|})}{\text{vol}(\Theta^{|\mathcal{S}|})} \in (0, 0.5),$$

where $\Theta^{|\mathcal{S}|}$ is the $(|\mathcal{S}|-1)$-dimensional closed unit sphere in dimension $|\mathcal{S}|$. Ecologically, this normalized feasibility domain can be interpreted as the probability of feasibility of a system $\mathcal{S}$ characterized by known pairwise interactions $\mathbf{A}$ under environmental uncertainty (all possible effective growth rates are equally likely to happen). The measure $F(\mathcal{S})$ can be efficiently estimated analytically (25, 42) or using Monte Carlo methods (Sec. S4). Moreover, $F(\mathcal{S})$ is robust to gLV dynamics with linear functional responses (25), a large family of nonlinear functional responses (41, 43), gLV stochastic dynamics (41, 43), and as a lower bound for complex polynomial models in species abundances (35).

Note that $F(\mathcal{S})$ always represents the feasibility of all $|\mathcal{S}|$ species together. That is, if a system (i.e., a given pool) is composed of 2 species or of 10 species, $F(\mathcal{S})$ represents the probability of feasibility of either 2 or 10 species, respectively (25). In the case where $|\mathcal{S}| = 2$, $F(\mathcal{S})$ corresponds to the traditional indicator of pairwise coexistence in isolation, which is proportional to what is typically known as niche overlap in gLV competition systems (44, 45). It is known that $F(\mathcal{S})$ will tend to decrease as a function of the dimension of the system (23, 35): $F(\mathcal{S}_1) > F(\mathcal{S}_2)$ if $|\mathcal{S}_1| < |\mathcal{S}_2|$. Thus, focusing on a given pair of species $\mathcal{Z} = \{x, y\}$ within a system $\mathcal{Z} \subset \mathcal{S}$, $F(\mathcal{S})$ will likely underestimate the probability of feasibility for the pair, whereas using only $F(\mathcal{Z})$ can be potentially misleading. For example, considering a pair that has a rather small feasibility domain in isolation ($F(\mathcal{Z}) \sim 0$, e.g., almost identical niches) will prompt us to conclude that the coexistence of this pair should be forbidden across all possible environmental conditions—as suggested by the checkerboard hypothesis (11, 14, 17). But, can this pair of species coexist more easily within a multispecies system (27, 28)? More importantly, will different pairs within the same system be equally benefited (or affected)?

Looking at traditional indicators from a systems perspective

To understand the extent to which $F(\mathcal{Z})$ provides a reliable indicator of the possibility of coexistence of a pair $\mathcal{Z} = \{x, y\}$ within a multispecies system $\mathcal{S}$ characterized by a pairwise interaction matrix $\mathbf{A}$, we study geometrically how the feasibility conditions $\boldsymbol{\theta}$ change when a pair of species is in isolation and within the multispecies system. Mathematically, the projection region D_{Proj} of the feasibility region D_F of a multispecies system $\mathcal{S}$ onto the 2-dimensional parameter space of a pair of species $\mathcal{Z}$ can be represented by the conical hull, i.e., the set of all conical combinations of the projection of spanning rays:

$$D_{\text{Proj}}(\mathcal{Z}, \mathcal{S}) = \left\{ \sum_{j \in \mathcal{S}} N_j^* \mathbf{b}_j : \mathbf{B} = [\mathbf{b}_1 \ \mathbf{b}_2 \ \cdots \ \mathbf{b}_{|\mathcal{S}|}], N_j^* \in \mathbb{R}_{>0} \right\} \in \mathbb{R}^2,$$

where $\mathbf{b}_j$ is the jth column vector of $\mathbf{B}$, and it contains a subset of elements corresponding to the pair $\mathcal{Z}$ in the column vector $\mathbf{a}_j$ of the interaction matrix $\mathbf{A}$. In other words, $\mathbf{B}$ consists of the row vectors $\mathbf{a}_i$ of $\mathbf{A}$ that correspond to the pair $\mathcal{Z}$ (i.e., $i \in \mathcal{Z}$). For example, for the pair of species 1 and 3 (i.e., $\mathcal{Z} = \{1, 3\}$), for each column vector $\mathbf{a}_j = (a_{1j}, \cdots, a_{|\mathcal{S}|j})^\intercal$, $j \in \{1, \cdots, |\mathcal{S}|\}$ in $\mathbf{A}$, we have $\mathbf{b}_j = (a_{1j}, a_{3j})^\intercal$ in $\mathbf{B}$. Then, we can obtain the normalized projection by the following ratio of volumes:

$$\text{Proj}(\mathcal{Z}, \mathcal{S}) = \frac{\text{vol}(D_{\text{Proj}}(\mathcal{Z}, \mathcal{S}) \cap \Theta^2)}{\text{vol}(\Theta^2)} \in [F(\mathcal{Z}), 0.5] \cup \{1\}.$$

Recall that $F(\mathcal{Z})$ is the feasibility of pair $\mathcal{Z}$ in isolation (using the corresponding 2-dimensional sub-matrix $\mathbf{A}[x, y; x, y]$).

If the projection region is not the entire 2-dimensional parameter space $\boldsymbol{\theta}$ of the pair, the projection ranges within Proj $\in (0, 0.5]$. Otherwise, Proj $= 1$, indicating that the region (θ_1, θ_2) incompatible with the possible coexistence of the pair disappears (Fig. 1A provides an illustration). In other words, pairwise coexistence can be possible under any combination of (θ_1, θ_2) depending on the other $\boldsymbol{\theta}$ values associated with the additional species in the system. In fact, per definition $D_{\text{Proj}}(\mathcal{Z}, \mathcal{S}) \geq D_F(\mathcal{Z})$, the entire projection region $D_{\text{Proj}}(\mathcal{Z}, \mathcal{S})$ defines equal or weaker constraints on the plane $(\theta_1,\ \theta_2)$ for the coexistence of the pair. Thus, the amount of *projection contribution* increasing the feasibility domain on the plane (θ_1, θ_2) can be defined as

$$PC(\mathcal{Z}, \mathcal{S}) = \frac{\text{Proj}(\mathcal{Z}, \mathcal{S})}{F(\mathcal{Z})}. \tag{1}$$

Because the combination of spanning vectors increases as the dimension of the system $|\mathcal{S}|$ grows, the projection $\text{Proj}(\mathcal{Z}, \mathcal{S})$ is expected to approach 1 in large multispecies systems (Figs. S3-S4).

Analytical system-level effects

To find long-term analytical indicators of pairwise coexistence within multispecies systems, first we propose to do a geometric partition of the feasibility regions of all possible species compositions within a multispecies system. Formally, in a multispecies system $\mathcal{S}$ with an interaction matrix $\mathbf{A}$, the feasibility region of a composition $\mathcal{C}$ ($\mathcal{C} \subseteq \mathcal{S},\ \mathcal{C} \neq \emptyset$) can be defined as:

$$D_F(\mathcal{C}, \mathcal{S}) = \left\{ \sum_{j \in \mathcal{C}} N_j^* \mathbf{a}_j - \sum_{k \in \mathcal{S} \setminus \mathcal{C}} N_k^* \mathbf{e}_k : \mathbf{A} = [\mathbf{a}_1\ \mathbf{a}_2\ \cdots\ \mathbf{a}_{|\mathcal{S}|}], N_{j,k}^* \in \mathbb{R}_{>0} \right\} \in \mathbb{R}^{|\mathcal{S}|},$$

where $\mathbf{e}_k$ is a unit vector whose k^{th} entry is 1 and 0 elsewhere. In fact, for a composition $\mathcal{C}$, we only need the subset of column vectors $\mathbf{a}_j$ of $\mathbf{A}$ corresponding to the community $\mathcal{C}$ (i.e., $j \in \mathcal{C}$) instead of the whole matrix. For example, for the species composition $\mathcal{C} = \{1, 2, 3\}$, only the 1st, 2nd and 3rd column vectors of $\mathbf{A}$ (i.e., the sub-matrix $[\mathbf{a}_1\ \mathbf{a}_2\ \mathbf{a}_3]$) are needed to define its feasibility region. Furthermore, we can define the normalized feasibility of a composition $\mathcal{C}$ by

$$F(\mathcal{C},\mathcal{S}) = \frac{\mathrm{vol}(D_F(\mathcal{C},\mathcal{S}) \cap \Theta^{|\mathcal{S}|})}{\mathrm{vol}(\Theta^{|\mathcal{S}|})} \in (0, F(\mathcal{C})].$$

Note that $F(\mathcal{C})$ is a function of the sub-matrix formed only by the interactions between the species in $\mathcal{C}$ (i.e., $\mathbf{A}[\mathcal{C};\mathcal{C}]$); while $F(\mathcal{C},\mathcal{S})$ is a function of this sub-matrix augmented by the system-level effects of the composition on the other species in the system. In general, $F(\mathcal{C},\mathcal{S}) = F(\mathcal{C})$ only when $\mathcal{C} = \mathcal{S}$.

Following our geometric partition, we define the probability of feasibility of a pair of species $\mathcal{Z}$ in a multispecies system $\mathcal{S}$ as the sum of all the feasibility regions where the pair forms part of the species composition ($\mathcal{Z} \subseteq \mathcal{C} \subseteq \mathcal{S}$):

$$P(\mathcal{Z},\mathcal{S}) = \sum_{\mathcal{Z}\subseteq\mathcal{C}\subseteq\mathcal{S}} F(\mathcal{C},\mathcal{S}).$$

Because the proposed probability of feasibility is related to the solution of the system at equilibrium, we estimate analytically the *long-term effect* of a multispecies system $\mathcal{S}$ on a pair $\mathcal{Z}$ by

$$LE(\mathcal{Z},\mathcal{S}) = \frac{P(\mathcal{Z},\mathcal{S})}{F(\mathcal{Z})}, \tag{2}$$

which represents the extent to which a system can modify the probability of pairwise coexistence relative to the probability of the pair in isolation allowing infinite time (Fig. 1B). Note that Eqn. (2) describes the effect of the multispecies system on the *probability* that the community $\mathcal{C}$ arises as a subcommunity of the full system, while Eqn. (1) denotes the effect of the multispecies system in weakening constraints on the range of parameters allowing *possible* coexistence of subcommunity $\mathcal{C}$.

Numerical system-level effects

While the long-term behavior of a multispecies system provides an expectation of its effect on a pair of species under an ideal setting; in practice, the study of pairwise coexistence in natural or experimental settings depends on the time scale of investigation, extinction thresholds, and the finite number of replicates. This implies that transient dynamics may play an additional role and observed coexistence rates may be different from the long-term expectations (12, 46). Thus, to provide a practical short-term perspective regarding the effect of a multispecies system on the probability of pairwise coexistence, we complement the analytical calculations of feasibility with numerical calculations. For each system, we simulate gLV dynamics over a given time interval across an arbitrary number of repetitions with arbitrary initial conditions (using Uniform$[0,1]$ for each species, but starting with the same abundance for all species yields similar results), effective growth rates $\boldsymbol{\theta}$ sampled randomly from the closed unit sphere, and classify species with a final abundance $N < 10^{-6}$ (results are robust to different thresholds) as statistically extinct (Fig. 1C).

We quantify the *short-term effect* of a system $\mathcal{S}$ on a pair of species $\mathcal{Z}$ by the ratio of the simulated

frequencies of pairwise coexistence at the system level and the simulated frequencies in isolation:

$$SE(\mathcal{Z},\mathcal{S}) = \frac{\mathrm{Sim}(\mathcal{Z},\mathcal{S})}{\mathrm{Sim}(\mathcal{Z})} = \frac{\#\ \mathcal{Z} \text{ in } \mathcal{S}}{\#\text{ simulations of } \mathcal{S}} \Big/ \frac{\#\ \mathcal{Z} \text{ in } \mathcal{Z}}{\#\text{ simulations of } \mathcal{Z}}.$$

Per definition, the simulated coexistence frequencies are always greater than or equal to the analytical, i.e., there is a short-term buffering effect $\mathrm{Sim}(\mathcal{Z},\mathcal{S}) \geq P(\mathcal{Z},\mathcal{S})$ and at $\mathrm{Sim}(\mathcal{Z}) \geq F(\mathcal{Z})$. Only after a sufficiently long time do the simulated and analytical frequencies become the same (Fig. S7).

To study whether the equilibration between short-term and long-term effects happens more quickly at the system level or in isolation, we quantify the *buffering effect* of a simulated system by the ratio between the short-term and long-term effects

$$BE(\mathcal{Z},\mathcal{S}) = \frac{SE(\mathcal{Z},\mathcal{S})}{LE(\mathcal{Z},\mathcal{S})} = \frac{\mathrm{Sim}(\mathcal{Z},\mathcal{S})}{P(\mathcal{Z},\mathcal{S})} \cdot \left(\frac{\mathrm{Sim}(\mathcal{Z})}{F(\mathcal{Z})}\right)^{-1},$$

which represents the transient benefit (if > 1) or disadvantage (if < 1) to a pair of species after a finite time simulation of the system dynamics relative to the expected long-term behavior in the analytical calculations. For a given pair, the value of the buffering effect can change according to the chosen criteria for the simulations (Fig. S10), particularly the time span of the simulation. Yet, $BE(\mathcal{Z},\mathcal{S}) = 1$ if the two simulated frequencies (within systems $\mathrm{Sim}(\mathcal{Z},\mathcal{S})$ and in isolation $\mathrm{Sim}(\mathcal{Z})$) are greater than their analytical counterparts (within systems $P(\mathcal{Z},\mathcal{S})$ and in isolation $F(\mathcal{Z})$) in equal proportion. On the other hand, if $BE(\mathcal{Z},\mathcal{S})$ is greater (resp. less) than 1, the buffering effect is stronger within the system (resp. in isolation).

Comparing analytical and numerical effects for a given pair

To illustrate how the long-term (analytical) and short-term (numerical) effects act on a given pair within different systems, Figure 1D shows the distribution of analytical and numerical system-level effects calculated on a hypothetical pair of symmetrically competing species $\mathcal{Z} = \{1, 2\}$ ($a_{12} = a_{21} = 0.22$) when assembled together with different third species. Here, the interactions associated with the third species are chosen randomly from a normal distribution with $\mu = 0$ and $\sigma = 1$ (all diagonal values are set to $a_{ii} = 1$). Note that for such systems there is generally a stable equilibrium, so $\mathcal{F}(\mathcal{S}) > 0$. First, in this example, the projection contribution (first pink distribution) displays a large range of values including its maximum 1, confirming that the necessary conditions in (θ_1, θ_2) for pairwise coexistence in isolation are substantially expanded within the system. Second, the long-term effects (second blue distribution) as well as the short-term effects (third orange distribution) show that the probability of pairwise coexistence within the system can either decrease or increase compared to the probability in isolation. Yet, both distributions are approximately centered at 1, especially for the analytical case (95% confidence intervals for the mean of analytical effects [0.956, 1.027]). In fact, Figure 1E shows that both effects are positively associated, but not perfectly correlated, as expected due to transient behavior. We have considered a wide variety of such systems and find that this

property is similar for any pair of species under various numbers of randomly-assembled additional species (Figs. S3-S4). This reveals that the probability of pairwise coexistence in isolation is very close to the expected probability across all possible (abiotic and biotic) conditions under both short-term and long-term behaviors. This result is confirmed and further illustrated by a perturbative analysis for weakly interacting systems in Sec. S5, where the center of the probability distribution of the analytical long-term effect varies from 1 only at fourth order in the interactions.

Lastly, for this particular pair of competing species, the buffering effects (fourth green distribution in Fig. 1D) are predominantly greater than 1, showing that the short-term effects tend to be stronger (relative to the long-term effects) within multispecies systems than in isolation. More generally, Figure 1F shows that negative (resp. positive) long-term effects of a system on pairwise coexistence are associated with a stronger (resp. weaker) buffering effect within systems than in isolation. In other words, short-term effects tend to be higher (resp. lower) than long-term effects if these long-term effects are less (resp. greater) than one. These results also hold for cases where the environmental effects are constrained to specific regions of the parameter space (Sec. S3, Fig. S6). All these results are also confirmed by the perturbative analysis for weakly interacting systems in Sec. S5.

Comparing analytical and numerical effects across pairs

Next, we study how the long-term (analytical) and short-term (numerical) effects act across pairs within a given system. Specifically, we randomly generate a five-dimensional interaction matrix $\mathbf{A}$, where the interspecific effects (off-diagonal values) are sampled using a normal distribution with $\mu = 0$ and $\sigma = 0.25$ (all diagonal values are set to $a_{ii} = 1$), making sure that the interaction matrix is diagonally dominant. These values and conditions are chosen for illustrative purposes in line with experimental data in Sec. S4, but results are robust to this choice (Figs. 2 and S9). Additionally, to study how patterns can change as a function of the level of competition in a system, we generate a different five-dimensional interaction matrix, where the elements are the same as the first matrix except that all the off-diagonal signs are inverted. Then, for each pair within these randomly-generated matrices $\mathbf{A}$, we calculate the projection contribution $PC(\mathcal{Z}, \mathcal{S})$, long-term effects $LE(\mathcal{Z}, \mathcal{S})$, short-term effects $SE(\mathcal{Z}, \mathcal{S})$, and the buffering effects $BE(\mathcal{Z}, \mathcal{S})$. Note that in order to calculate the simulated frequency of coexistence of each pair in isolation $\mathrm{Sim}(\mathcal{Z})$, we run simulations at the pair level using the corresponding two-dimensional sub-matrices $\mathbf{A}[x, y; x, y]$ and sub-vectors $\boldsymbol{\theta}[x, y]$.

Figures 2A-2B and 2C-2D summarize our results for a pair of negative-dominated ($-\langle a_{ij} \rangle = -0.051$) and positive-dominated ($-\langle a_{ij} \rangle = 0.051$) interaction matrices, respectively. First, we found that the projection contribution (first pink distribution) is highly heterogeneous across pairs. Recall that this is a function of the combination between the pairwise interactions in $\mathcal{Z}$ and the remaining interactions in the system $\mathcal{S}$, where this combination changes from pair to pair. Second, we found that the long-term effects (second blue distribution) and short-term effects (third orange distribution) of multispecies systems can be disadvantageous (< 1) or beneficial (> 1) for pairs. Importantly, these effects are

not equal across all pairs within the systems. Note that these distributions are only expected to be centered close to 1 for large enough systems given that each point in these distributions corresponds to a different pair within a fixed system (not a fixed pair within different systems as in Fig. 1D). Third, the buffering effects (fourth green distribution) show values predominantly greater than (resp. less than) one in Figure 2A (resp. Figure 2C), revealing that the short-term effects tend to be stronger (resp. weaker) within systems than in isolation under negative-dominated (resp. positive-dominated) interactions. Note that these strong (resp. weak) buffering effects are generated by the system that also causes negative (resp. positive) effects over the long term.

To differentiate how long-term and short-term behaviors operate on each pair within a given system, we construct a cartographic representation (40) of the relationship between long-term and buffering effects. Figures 2B and 2D show that the majority of pairs tend to be negatively ($LE < 1$) and positively ($LE > 1$) affected over the long-term within negative-dominated and positive-dominated random matrices, respectively. As a mirror image, the majority of pairs tend to be positively ($BE > 1$) and negatively ($BE < 1$) affected over the short-term within negative-dominated and positive-dominated random matrices, respectively. That is, on average, negative (resp. positive) long-term effects of a system on pairwise coexistence are typically linked with a stronger (weaker) short-term buffering effects within systems than in isolation, in agreement with the general results found in the previous section for a fixed pair in a variety of environments. Note that this cartographic representation can change as a function of the time span of the simulation (see Fig. S10). These effects were not correlated with pairwise coexistence in isolation (the size of points is not associated with the value of either axis).

Experimental framework

Experimental data

To test our theory in a more realistic setting, we use a publicly available data set of an *in vivo* gut microbial system. The data set (hereafter the fruit fly data set) was generated in Ref. (15) and it comprises a set of ten-day experimental trials of five interacting microbes commonly found in the fruit fly *Drosophila melanogaster* gut microbiota: *Lactobacillus plantarum* (Lp), *Lactobacillus brevis* (Lb), *Acetobacter pasteurianus* (Ap), *Acetobacter tropicalis* (At), and *Acetobacter orientalis* (Ao). This in vivo experimental study performed monoculture experiments for each species, co-cultures experiments for each pair, and poly-culture experiments for the quintet (Fig. 3 provides an illustration), as well as triplet and quartet experiments not relevant to our analysis here. Each experiment was replicated 48 times across different hosts and each species' density was measured at the end of the observation period, providing one single record of persistence per replication for each species in monocultures, co-cultures, and poly-cultures (see Sec. S1 for details).

Experimental system-level effects

To investigate the system-level effects on pairwise coexistence using the in vivo data, for each pair $\mathcal{Z}$, we compute the empirical frequency of coexistence within a multispecies system $\mathcal{S}$ (i.e., within quintets) and in isolation $\mathcal{Z}$ (i.e., within pairs) separately. To determine species coexistence, we classify a species statistically extinct in a trial if its relative abundance was less than 1% at the end of the observation period. We also test different extinction thresholds and obtain qualitatively the same results (Fig. S12). We define the *experimental effect* of the system on pairwise coexistence as the ratio between the frequency of coexistence within a system and the frequency in isolation (Fig. 3 provides an illustration):

$$EE(\mathcal{Z},\mathcal{S}) = \frac{\#\ \mathcal{Z} \text{ in } \mathcal{S}}{\#\text{ replicates of } \mathcal{S}} \Big/ \frac{\#\ \mathcal{Z} \text{ in } \mathcal{Z}}{\#\text{ replicates of } \mathcal{Z}}.$$

To compare the experimental and long-term (analytical) effects, we use the experimentally-inferred five-dimensional pairwise matrix $\mathbf{A}$ (see Sec. S2 for more details). This matrix was characterized by negative-dominant interactions ($-\langle a_{ij}\rangle = -0.078$). Using this experimentally-inferred matrix, we analytically calculate the projected contributions $PC(\mathcal{Z},\mathcal{S})$ and long-term effects $LE(\mathcal{Z},\mathcal{S})$ of the system with $|\mathcal{S}| = 5$. We chose the quintet experiment (instead of the triplets or quartets) in order to have more pairs (10 with fives species) to perform statistics. In line with our numerical analysis, the *experimental buffering effect* $EBE(\mathcal{Z},\mathcal{S})$ is calculated by the ratio between the experimental effect $EE(\mathcal{Z},\mathcal{S})$ and long-term effect $LE(\mathcal{Z},\mathcal{S})$. We also construct a cartographic representation of the relationship between long-term effects and the experimental buffering effect in order to differentiate how long-term (analytical) and short-term (experimental) behaviors operate on each pair within the experimental system.

Comparing analytical and experimental effects across pairs

We found that the experimental system-level effects on pairwise coexistence were very similar to those generated by simulations (Figs. 2 and 4). Specifically, Figure 4A shows that the experimental multispecies system generated heterogeneous effects across pairs as illustrated by a wide distribution of projection contributions (first pink distributions), long-term effects (second blue distributions), and experimental effects (third orange distributions). Similar to simulations for systems with negative-dominant interactions, the in vivo experimental system shows predominately positive values of buffering effects (fourth green distributions). This shows that despite the negative long-term effects of the system of pairwise coexistence, there is a stronger buffering effect at the system level than in isolation. Focusing on the cartographic representation of differences among pairs, Figure 4B shows that the majority of pairs tend to be negatively affected over the long-term ($LE < 1$) and positively affected over the short-term ($EBE > 1$)—consistent with the results obtained for negative-dominant matrices (Fig. 2B). This cartographic representation can also help to understand specific pairwise cases. For

example, the pair (Ap, At) was observed with negative long-term effects but with a strongly positive buffering effect over the short-term (top left region). In contrast, the pair (Lp, Ap) exhibited the complete opposite effects. In turn, the pair (Ap, Ao) exhibited positive effects over both the long-term and short-term, suggesting that this pair is substantially benefited by the system. Note that this classification can change as a function of the experimental details. Importantly, these effects were again uncorrelated with pairwise coexistence in isolation (the size of points in Fig. 4B is not associated with the value of either axis), confirming the importance of systems dynamics on pairwise coexistence.

Conclusions

A major challenge in ecological research has been understanding how species interactions and heterogeneous environments affect the opportunities for species coexistence (2, 4). Many research efforts have been devoted to study the coexistence of either two species in isolation or that of a particular set of multiple species (8). Yet, species are seldom in isolation and the coexistence of a specific combination of multiple species is expected to be rare in a random environment (5, 24, 25). This has prompted us to better understand the extent to which the coexistence of a particular pair or group of species can change between being in isolation to being part of a larger system. This is also a critical focus and challenge in bio-restoration and bio-medicine, where it is unclear whether a large system can have different effects on its different pairs of species (6, 7, 47–49). The main problem resides in the fact that in natural settings, most of the abiotic and biotic effects acting on species are unknown. As a response to this problem, we have introduced an analytical formula to estimate the extent to which a given multispecies system (more than two species) can affect the probability that a particular pair of species coexist under environmental uncertainty (all possible conditions are equally likely to happen). This formula is based on information about pairwise interactions from a given pool of species and assumes that the total effect of all additional biotic and abiotic factors can be captured by a phenomenological random parameter for each species (i.e., the effective growth rate parameter θ)

Following our analytical framework, we have shown that the diversity of multispecies systems opens the opportunity for pairwise coexistence regardless of whether a given pair can coexist or not in isolation. This phenomenon occurs since the environmental conditions limiting the coexistence of a pair in isolation (parameter values acting on a plane) is replaced by a new set of conditions acting on all species, whose projection onto the two-dimensional space tends to cover the pair's entire plane. Thus, the possibility of pairwise coexistence in a multispecies system only depends on the new set of conditions in the multi-dimensional space of the entire system. In contrast, the fraction of conditions (probability) in the multi-dimensional space can be less or greater than the probability in isolation, depending on the pairwise interactions that characterize the multispecies system. Importantly, under environmental uncertainty, the expected value of the distribution of probabilities generated by all possible multispecies systems is approximately the same as the probability in isolation. This reasoning can be applied to any group of species in multispecies systems, implying that even without knowl-

edge about all the abiotic and biotic factors that may affect a particular set of species, we can have a good approximation to their coexistence expectation using minimum information about pairwise interactions.

While analytical measures are useful for increasing our general understanding of pairwise coexistence, the assumptions behind these measures may never be met in real-wold systems. For example, our analytical measures are based on the long-term asymptotic equilibria achieved by systems in arbitrary environmental conditions. Yet, both simulations and experiments are always restricted to or biased by short-term (finite) effects. Hence, to provide an additional understanding of such short-term effects, we have compared our analytical expectations against numerical and experimental outcomes. As expected, we have found that the probability of pairwise coexistence over the short term (numerically and experimentally) is greater than pairwise coexistence over the long term (12). Yet, it has been unclear whether this buffering effect should be equal in both multispecies systems and in isolation. We have found that this increase is typically greater (resp. smaller) for pairs in multispecies systems than in isolation if the system affects the pairs negatively (resp. positively) in the long term. This illustrates potential differences to what we may see in experiments and the expected long-term dynamics of ecological systems. Moreover, these effects are not equal across all pairs within a system. Importantly, we have shown that we can study these differences using a cartographic representation of how a system is expected to affect the long-term and short-term behavior of each pair.

As a final note, it is worth mentioning that our theory assumes that environmental conditions are uniformly distributed across the entire parameter space. Instead, under experimental settings, much stronger constraints on environmental conditions can be expected. This implies that the probability of pairwise coexistence should be different between theoretical and experimental analyses. Yet, these experimental constraints should also be expected to operate on pairs in both multispecies systems and in isolation. Therefore, system-level effects (ratio between the probability in multispecies systems and in isolation) should be comparable between theoretical and experimental analyses. Indeed, our theoretical analysis (Fig. 2) showed similar patterns to the experimental analysis (Fig. 4), suggesting that our phenomenological framework is applicable to real-world settings and can be used to increase our understanding about long-term and short-term dynamics.

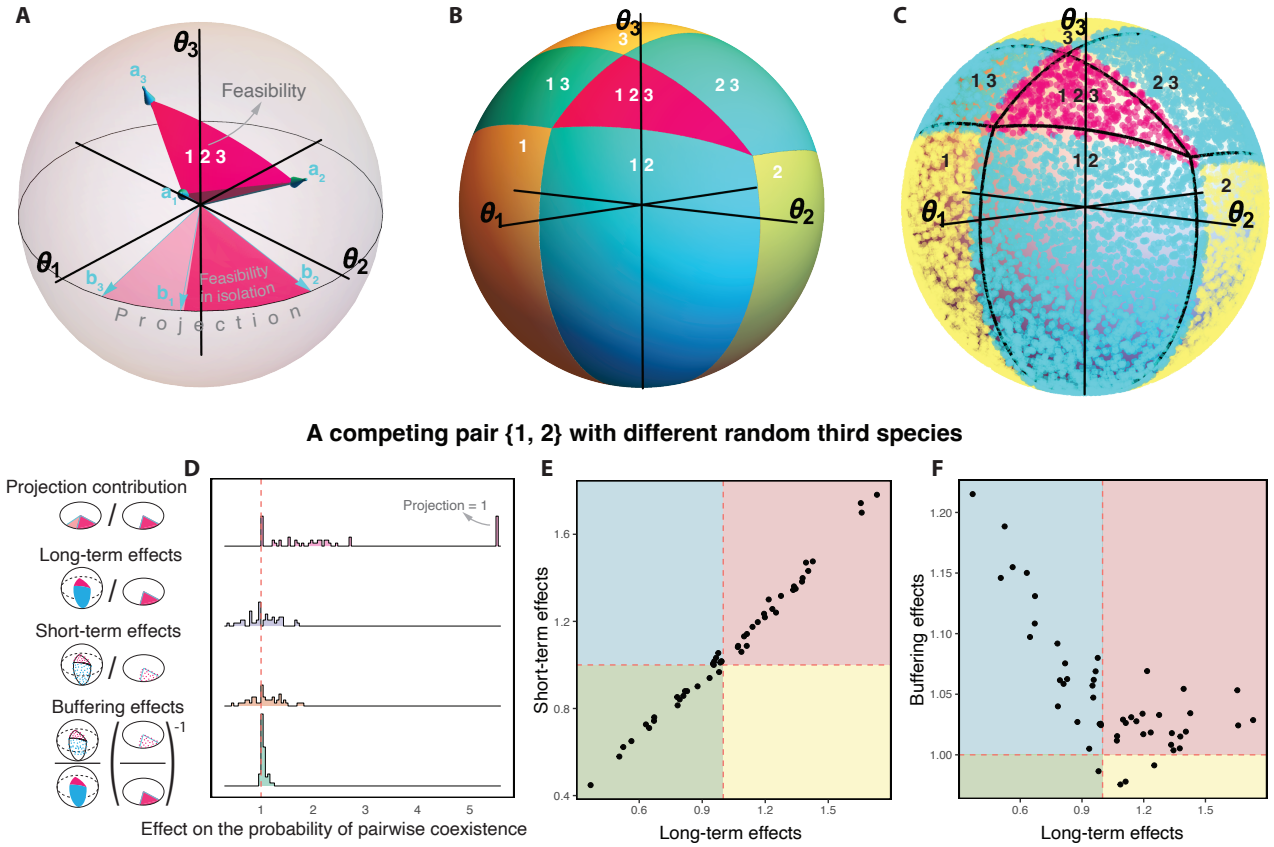

Figure 1: **Geometric perspective of the effect of a system on pairwise coexistence.** For a fictitious system of three species, Panel **A** shows the geometrical representation of the feasibility region $D_F(\mathcal{S})$ (i.e., pink cone spanned by $\mathbf{a}_1,\ \mathbf{a}_2,\ \mathbf{a}_3$) of an illustrative three-species system $\mathcal{S}$ characterized by the interaction matrix $\mathbf{A} \in \mathbb{R}^{3\times 3}$ in the three-dimensional space of effective growth rates $(\theta_1,\ \theta_2,\ \theta_3)$. The panel also shows the projection $D_{\text{Proj}}(\mathcal{Z}, \mathcal{S})$ of the spanning rays onto the two-dimensional plane $(\theta_1,\ \theta_2)$ of the pair $\mathcal{Z} = \{1, 2\}$ (i.e., light pink disk spanned by $\mathbf{b}_2,\ \mathbf{b}_3$). The feasibility of pair $\{1, 2\}$ in isolation (i.e., a 2-species pool) $D_F(\mathcal{Z})$ is given by $\mathbf{b}_1,\ \mathbf{b}_2$ (i.e., dark pink disk), and becomes a fraction of the projection corresponding to the possible coexistence of species 1 and 2 only. Panel **B** illustrates the geometric partition of the analytical feasibility regions of all possible compositions in the previous three-species system. For the same system, the points in Panel **C** show the resulting species composition (species with final abundances $N < 10^{-6}$ are considered statistically extinct) from 10,000 simulations over a short finite time interval (total time = 200, step size = 0.01). Note that these results are a function of the time span of simulations (see Fig. S7). The black lines correspond to the borders of the analytical feasibility regions in Panel **B**. Panel **D** shows the distribution of system-level effects calculated on a fixed hypothetical pair of symmetrically competing species $\mathcal{Z} = \{1, 2\}$ when assembled with different random third species. The distributions are generated using 50 random third species (see text for details). Each point in the distributions corresponds to the same pair in a different system. For reference, the dashed line shows the value of one: the relative feasibility in isolation. Panels **E-F** show the positive and negative association of the long-term effect with the short-term and buffering effects, respectively (Panel **E**: Pearson's product-moment correlation = 0.995, p-value < 0.001; Panel **F**: Pearson's product-moment correlation = -0.707, p-value < 0.001). These results are complemented by a perturbative analysis for weakly interacting systems in Sec. S5.

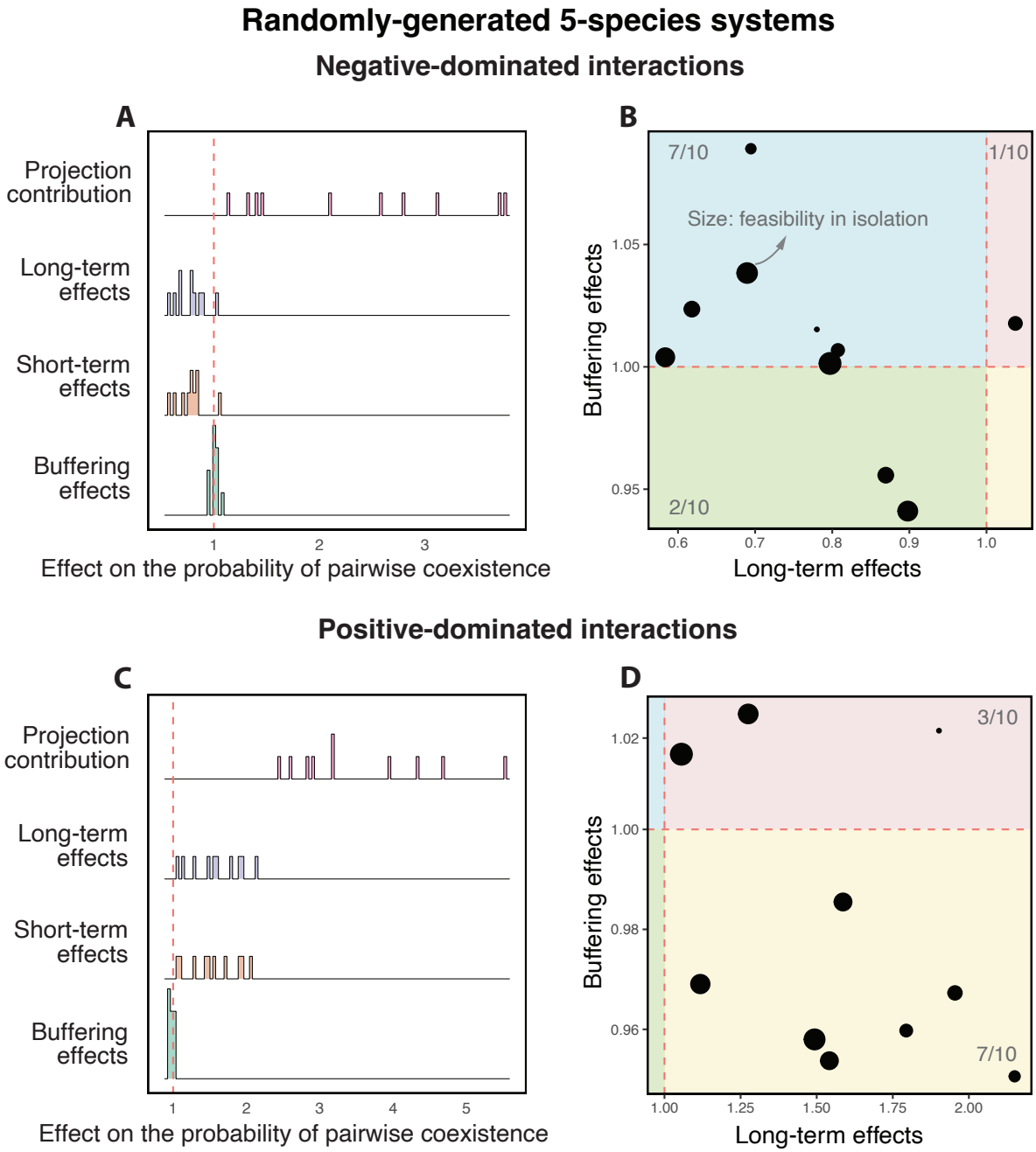

Figure 2: **Cartographic representation of long-term and short-term differences among pairs within the same system.** Panels **A** and **C** show the system-level effects on 10 pairs within a randomly-generated five-species system characterized by negative-dominated and positive-dominated interactions, respectively (see text). Rows correspond to the projection distribution ($PC(\mathcal{Z},\mathcal{S})$), long-term effects ($LE(\mathcal{Z},\mathcal{S})$), short-term effects ($SE(\mathcal{Z},\mathcal{S})$), and buffering effects ($BE(\mathcal{Z},\mathcal{S})$), respectively. Note that each point in the distributions is a different pair within a system. For reference, the dashed line shows the value of 1. Recall that the x-axis corresponds to the change in probability of pairwise coexistence within the system. Panels **B** and **D** illustrate the cartographic representation for all corresponding pairs based on beneficial ($LE(\mathcal{Z},\mathcal{S}) > 1$) or detrimental ($LE(\mathcal{Z},\mathcal{S}) < 1$) long-term effects and beneficial ($BE(\mathcal{Z},\mathcal{S}) < 1$) or detrimental ($BE(\mathcal{Z},\mathcal{S}) < 1$) short-term buffering effects. The size of points corresponds to the feasibility of pairs in isolation. The number of points in each region is annotated in gray. See Fig. S9 for a ten-species system.

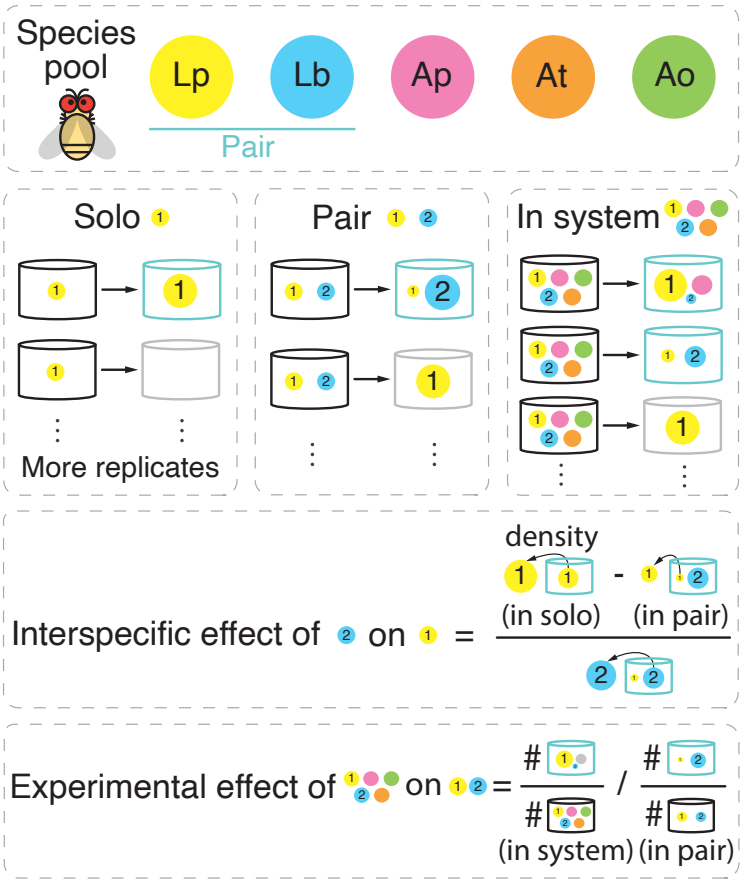

Figure 3: **Illustration of experimental data, inference of pairwise interactions, and calculation of experimental effects.** We use publicly available data of an *in vivo* gut microbial system. The data set was generated in Ref. (15) and it comprises ten-day experimental trials of five interacting microbes commonly found in the fruit fly *Drosophila melanogaster* gut microbiota: *Lactobacillus plantarum* (Lp), *Lactobacillus brevis* (Lb), *Acetobacter pasteurianus* (Ap), *Acetobacter tropicalis* (At), and *Acetobacter orientalis* (Ao). From the available experimental data, we used the results from monoculture experiments for each species, co-cultures experiments for each pair, and poly-culture experiments for the quintet. Each experiment was replicated across different hosts and each species' density was measured at the end of the observation period, providing a single record of persistence for each species in monocultures, co-cultures, and poly-cultures per replication. The experimentally-inferred pairwise matrix $\mathbf{A}$ was inferred using the data of monoculture experiments for each species (e.g., species 1) and co-cultures experiments for pairs (e.g., pair $\{1, 2\}$) by evaluating the modified abundance of species 1 with and without species 2 at the end of the observation periods (see Sec. S3). We define the experimental effects of the multispecies system on pair $\{1, 2\}$ as the difference in the experimental frequencies of occurrence of the pair across all replicates within multispecies system and the experimental frequencies of occurrence of the pair in isolation.

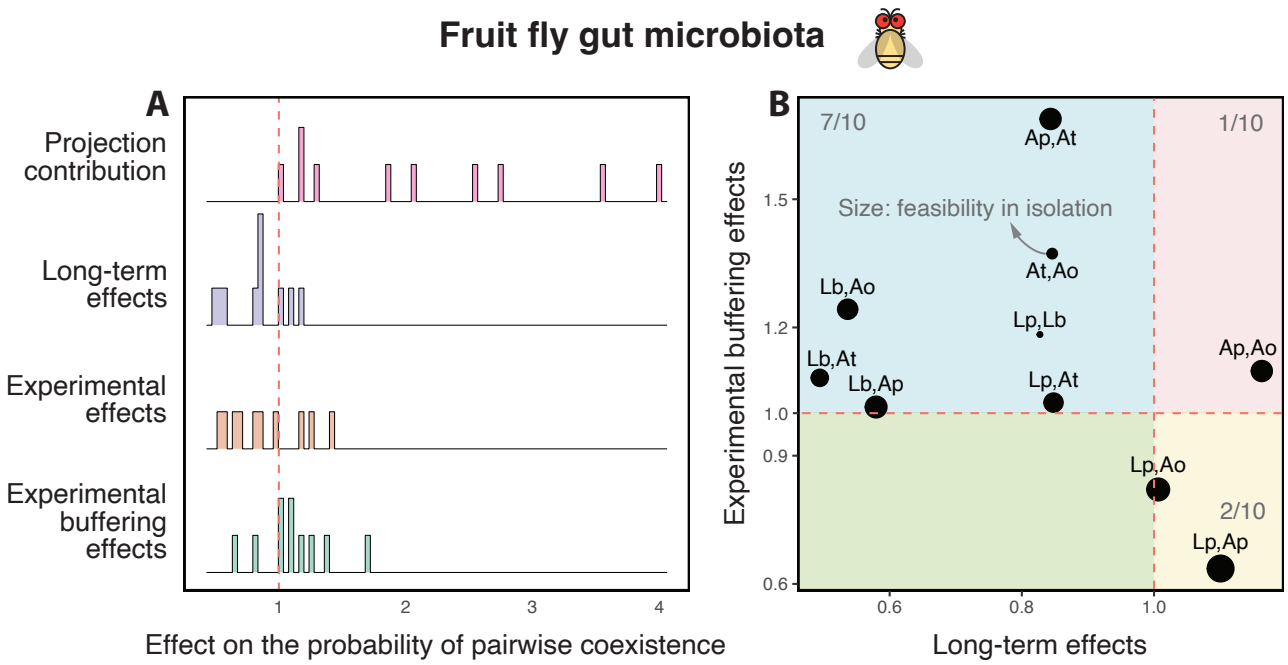

Figure 4: **Comparing system-level effects among pairs within a five-species in vivo experimental system.** This figure shows similar information to Fig. 2, but using the experimental data and the experimentally-inferred interaction matrix. For each of the 10 pairs in the experimental fruit fly system, Panel **A** shows the projection distribution $PC(\mathcal{Z}, \mathcal{S})$ (first row pink distribution), long-term effects $LE(\mathcal{Z}, \mathcal{S})$ (second row blue distribution), experimental effects $EE(\mathcal{Z}, \mathcal{S})$ (third row orange distribution), and experimental buffering effects $EBE(\mathcal{Z}, \mathcal{S})$ (fourth row green distribution). Panel **B** shows the cartographic representation of how the system affects the long-term and short-term behavior of each of its constituent pairs. Long-term effects can be beneficial ($LE(\mathcal{Z}, \mathcal{S}) > 1$) or detrimental ($LE(\mathcal{Z}, \mathcal{S}) < 1$). In this experimental system, the majority of short-term effects tend to be beneficial ($EBE(\mathcal{Z}, \mathcal{S}) < 1$) in line with negative-dominated interaction matrices (Fig. 2B). See text or Fig. 3 for all species names.

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