# Preamble

## Proposed Titles

* **Consumer resource competitive model identifies the community assembly scenarios that lead to negative effects in Biodiversity Ecosystem Function relationships**
* **Community assembly scenarios that lead to negative effects in Biodiversity Ecosystem Function relationships**
* **When to expect negative effects in Biodiversity-Ecosystem Function relationships?**
* **A jack of all trade-offs is hard to find: the rarity of negative biodiversity-ecosystem function relationships**
* **Increased richness rarely leads to lower function in pitcher plant microbial communities**
* **When biodiversity has a negative impact on ecosystem function: insights from pitcher plant microbial communities** (Rafael’s vote, Gabriel’s vote)
* **When biodiversity has a negative impact on ecosystem function: insights from a consumer-resource model** (Leonora’s vote, Thomas’ vote)
* **I think a good title would be one that tells the main take-home message, perhaps?**

**ROLES**

* Catalina is the official leader of the project.
* Catalina and Rafael are the main contributors to the manuscript/results
* Gabriel and Thomas are consultants and help polish the writing and verify soundness of results
* Veronica provides big-picture perspective and makes sure paper has broader appeal
* Leonora Bittleston provides pitcher plant insights and empirical data, writes part of the Box and helps with general concepts and editing

## Outline

VF: It is better to keep a consistent pattern across the entire paper since we are covering a variety of components within this BEF investigation and it can be helpful to the reader to follow. So, because the model and the results are presented in the order of (1) community relationships/scenarios, (2) mechanisms, and (3) negative BEF direction, then all other written parts should follow that same order (intro, methods, results, discussion). This also seems to be the “funnel” idea of writing-from broad to narrow. Below is a new outline to follow this kind of thinking. The information is mostly in the manuscript already, but I am just reordering it. Since Catalina is not able to make edits this month, you will see that I made direct changes to the intro instead of suggestions. Other parts are suggested edits.

**For each paragraph, I will note in red the theme/aim of the paragraph so it can help us as we try to guide the reader.**

1. Introduction
   1. General need (1 paragraph)
      1. Need statement: Despite decades of studies linking diversity and function, in order to better manage and predict changes in these relationships, a general, mechanistic framework for exploring and explaining the variation in BEF relationships is still needed (Mouquet et al 2015)
   2. What determines the shape of a BEF, what we know so far, and what we still need to learn (3 paragraphs) - in some sense, we can have order to it, or we can just go with the organic order that is already written, but we still need to make sure that what we address in terms of state of knowledge will also link to the gaps and then link to what we hope to address for the paper.
      1. community relationships/scenarios
         1. Overview of community assembly and BEF
         2. What we know about them regarding BEF relationships
      2. mechanisms
         1. Overview of complementarity, selection, redundancy
         2. What we know about them regarding BEF relationships
      3. frequency of BEF directions (we are still missing this in the intro; we have a bit)
         1. Overview of frequency of positive, negative, neutral
         2. What we know about them regarding BEF relationships
         3. Is this the best place to refer to Box 1??? Or maybe Box 1 should be in the discussion?? The only reason to have this here is if we want the rarity of negative BEFs to be the central piece of this paper, but it doesn’t seem that way at the moment…
   3. Problem statements: overall, considering these 3 components, what is lacking? Ideally, we list things that we ourselves are also able to address in this paper. (1 paragraph)
      1. Limited study systems that fail to apply across other systems
      2. Something lacking in both experiments and observations???
      3. Something lacking in the theoretical side???
      4. End with a statement speculating/hypothesizing to lead into the proposal (next paragraphs)
   4. In this paper we do XYZ… (2 paragraphs)
      1. What we propose to accomplish
      2. How we do it
      3. Why it’s amazing (emphasis of the approach and why it’s advantageous, the scale of the factorial design [this was big!!!!], hints about discussion/broad impacts, making a point that this is not just a study about microbes or pitcher plants)
2. Methods
   1. Methods summary
      1. Description of microbial communities in pitcher plants (with citations), and refer to Figure 1
      2. Tools used (R v. 4.3? and packages) and refer to GitHub/Zenodo links
   2. Overall setup
   3. Simulations/factorial design
      1. Community
      2. Mechanisms
      3. BEF relationship direction
      4. We need numbers… how many simulations were done??? Listing big numbers (in abstract, too!!) will make high impact obvious
   4. Analysis
      1. What is extracted for interpretation and how it is analyzed (preparing the reader to receive the results the way they will be plotted)
      2. Random Forest
3. Results
   1. Community
   2. Mechanisms
   3. Rarity of negative BEF relationships
4. Discussion
   1. Summary of the findings and what was achieved (1 paragraph)
   2. Relationship (1 paragraph per component?)
      1. Major lessons learned and tie to real world
   3. Mechanism (1 paragraph per component?) (major lessons learned)
      1. Major lessons learned and tie to real world
   4. Rarity of negative BEF (major lessons learned)
      1. Major lessons learned and tie to real world
      2. I think Box 1 should be in the Discussion instead, but let’s wait and see…
   5. Promise/benefits of the model/work as a whole
      1. Pitcher plant microbial communities as an exemplary system
         1. Similar systems that can be considered so we do not limit the reader to thinking this is only about one system
      2. Mathematical model versus experiment or field work
      3. Broader applications to tie into the first paragraph of introduction (we might need a Box 2 to make it easier???)
   6. Limitations
      1. Critique, but also motivation for future work to expand on this framework (new ideas!)
         1. Scale tends to be a big issue in ecology, and we don’t address that here
      2. Remaining questions and future applications
5. Conclusion
   1. What is our major take-home message?

## Paper to-do list (add, comment, and check off as you wish)

* Terminology - make sure that key words used in methods/results match. Words to watch out for are:
  + “Recalcitrance”. Are we still using that word or did we decide against it?
  + “Seeded richness” is used in results but not in the methods or table S1
  + “nested by-production network” is in results but methods says just “byproduction scenarios.” The word “network” isn’t used at all in methods.
  + “satiation rates” is used in results but this has not been introduced in the methods or Table S1.
  + “Consumers” not introduced in methods but in results (is this strain i? Or species i?; should we change species to “consumers”?)
  + “resource index.” not introduced in methods
* Framework schematic explanation - needed in methods, but also there are **mismatches between methods, Figure 1, and the results**.
  + Fig 1B and 1C
    - ~~These processes are not labeled, but would be helpful for understanding the methods and the factorial design. (e.g. inhibition 1C is not considered a distinct scenario but it does get modified in the methods across simulations)~~
  + Fig 1D
    - ~~Change order to match Figure 2-3,5, and supp. (i.e., generalists on left, specialists in middle, and gradient on right)~~
    - ~~Is “uptake rates” the right title? Maybe the title should actually be the name for the scenario itself? (i.e., “niche scenario”, right?)~~
  + Fig 1E
    - ~~We are missing a visualization of “byproduction architecture,” but according to the methods/results, this is a scenario, too. Should have 3: none, nested, serial~~
    - Label should be called “By**-**production architecture scenarios”, with this order to match Figure 3: none, nested, serial
  + Fig 1F
    - The order of Fig 1F should match order in results: absent, neutral, intraspecific, interspecific
  + Fig 1G
    - Label should be called “Resource recalcitrance scenarios”
    - It would be good to label each of the scenario graphs so they can match what we are calling the efficiency scenarios in the methods/results (i.e., decrease, flat, increase) (check results figures to ensure that the labeling is in the same order as legends)
  + Fig 1H
    - Label should be “resource quality scenarios”
    - Graphs should have labels to match order in results figure legends and in same order: neutral, gradient
  + **Methods**
    - Resource quality, handling time, and efficiency all sound like different scenarios, but are they different or part of the same thing (Fig 1E)??
    - Table S1 and Methods need to match (scenarios, vocabulary, terms, etc).
  + **Results**
    - Make sure that the order of the settings for each scenario match the order in Figure 1. I think it’s easier to change Figure 1 to match the order of items in other figure legends than it is to do the reverse.

## Notes for high-impact as we write/edit

* Numbers/scale. Important to emphasize the scale of what has been done. Factorial design, numbers of simulations per species per scenario. Big numbers are part of the selling point for high-impact journals. This is also what makes the work unique and advantageous compared to experimental/observational research.
* Broad need, and broad applications of what was done.
* First sentence of most paragraphs (>90%) is the key or most important point of the entire paragraph. What is the goal of this paragraph? What is the take-home message? What is shocking?
* Subheadings throughout methods, results, discussion
* Figure captions need the most important message as the first sentence (the bold part) as opposed to a description of what it is. For the rest of the figure text, list the most important findings for the respective figure in addition to how to interpret components (colors, shapes, columns, etc).

# Title page

## Article title

???

## Running title

???

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## Key words

Biodiversity-ecosystem function, community assembly, microbial metabolic networks, pitcher plants, complementarity

## Statement of authorship

CCG, RD, TK, and GK designed the study, RD performed modeling work and analyzed output data, GK performed the random forest analysis, CCG contributed the wastewater treatment data, LB contributed the *S. sarracenia* microcosm data, VF outlined the manuscript, CCG and RD cowrote the first draft, and all authors contributed substantially to revisions.

## Data accessibility statement

All code used in simulations and data analyses is published on GitHub. Files for all raw simulated data are published in Zenodo (DOI CITATION). What about the Box 1 data?

## Article information

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# Abstract

The relationship between biodiversity and ecosystem function (BEF) is a core concern of community and ecosystem ecology. Despite decades of research, ecologists still lack a clear understanding of the causes of negative BEF and why they seem rare in nature. Here, we develop a consumer-resource dynamic model to investigate BEF in a microbial decomposer community in pitcher plant leaves. We manipulate microbial diversity via controlled colonization and measure their function as total ammonia production. We test how niche partitioning among bacteria and other ecological factors influence BEF in the leaves. We find that while positive or redundant BEF are the most common outcome, a negative BEF can emerge from density-dependent inhibition in ammonia production across species (co-regulation) causing a negative complementarity effect, or from competitive hierarchies causing a negative selection effect. Our findings align with empirical data on the rarity of negative BEF and shed light on its causes.

### 

# Introduction

The current accelerating biodiversity crisis has sparked a renewed interest in the relationships between biodiversity and ecosystem function, as species losses may lead to dramatic changes in the functioning of ecosystems that support human societies and, broadly, life on Earth (Cardinale et al 2012, Auber et al 2022, Srivastava and Vellend 2005). A large body of experimental, empirical, and theoretical evidence suggests that species-rich communities can support higher levels of ecosystem functioning (Balvanera et al 2006, Worm et al 2006, Hooper et al 2005, 2012). This positive biodiversity-ecosystem function (BEF) relationship forms the foundation of many conservation and sustainability efforts, recognizing that biodiversity is critical for maintaining fundamental ecosystem services (Loreau et al 2001, Tilman et al 2014, Naeem et al 1994, Tilman and Downing 1994). However, recent work reveals that positive BEF relationships are not universal (Hagan et al 2021, Hillebrand and Matthiessen 2009, van der Plas 2019). Instead, many systems show functional redundancy at even relatively low diversity levels (flat BEF relationships; Balvanera et al 2006), and, in rare cases, increases in diversity can even lead to a decrease in ecosystem function (negative BEF relationships; Jiang et al 2008, Peter et al 2011, Dee et al 2023, Box 1). Despite decades of studies linking diversity and function, we still need to better understand the causes of variation in BEF relationships (Mouquet et al 2015), and in particular the causes of negative BEF relationships, in order to better manage and predict changes in these relationships.

BEF relationships result from the combined effect of three mechanisms: complementarity, selection, and redundancy. Positive complementarity occurs when species in mixture yield higher function on average than when in monoculture due to niche packing or facilitation (Huston et al 1997, Loreau and Hector 2001). The opposite scenario, where species interfere with each other’s functional output when in mixture, would constitute negative complementarity. Selection happens when adding more species to a community increases the likelihood of including highly functional dominant species (Loreau 2000, Loreau and Hector 2001). A positive selection effect occurs when functionally dominant species are also superior competitors (Loreau 2000, Veen et al 2018, Doherty et al 2011), while negative selection effects occur when functionally active species are poor competitors that tend to be excluded from diverse assemblages (Jiang et al 2008, Peter et al 2011, Cuellar-Gempeler in prep). Redundancy occurs when function initially increases with biodiversity but reaches a point where any additional species are functionally redundant, and thus any further increase in diversity would not result in further functional increases (this is also called the “Insurance effect”, since it can buffer function from biodiversity loss, Yachi and Loreau 1999). While we know that complementarity and selection can contribute to positive and negative BEFs, and redundancy leads to flat BEF relationships, we do not know under what circumstances either mechanism will dominate and drive the resulting shape of the BEF relationship. Without this understanding, ecologists cannot explain why different BEF patterns appear unevenly in nature.

In a recent meta-analysis, van der Plas (2019) shows that positive BEF relationships outnumber negative BEF relationships in naturally assembled communities, while flat BEF relationships seem to be the most common across habitats, focal groups, and types of functions. The rarity of negative BEF relationships when compared to positive or redundant BEF in the literature can have two possible explanations: either they are intrinsically rare because the underlying mechanisms are unlikely, or studies are biased towards experimental designs or systems that do not portray negative BEF relationships (Jiang et al 2007). This constitutes a critical gap in knowledge regarding how species contribute to different ecosystem functions and how community assembly may impact the diversity-function relationship. Here, we aim to address this gap using a resource competition model and explicit assembly dynamics. The goal is to broaden our understanding of the mechanisms underlying BEF relationships, with a focus on understanding which ecological scenarios increase the likelihood of negative BEF relationships.

Traditional approaches to modeling BEF relationships focus on primary productivity in plant communities, with productivity typically assumed proportional to biomass and nutrient acquisition (Loreau 1998, Tilman et al 1997, Morin 2011). While this approach may capture BEF relationships in many communities, it disregards important complexities in how species within many other types of communities can contribute to function. One important example are microbial communities, where competitive dominance via resource use specialization (D'’ouza et al 2018, Pande and Kost 2017, Seth and Taga 2014), resource exchange via release of metabolic by-products to the media (cross-feeding), and co-regulation---when a species influences another species’ ability to uptake and process resources (Freilich et al 2011, Lacombe-Harvey et al 2018) likely affect relationships between species diversity and ecosystem function. These processes can have important consequences for community assembly and ecosystem function alike, and yet have not been incorporated into the BEF framework. We hypothesize that these mechanisms, alone or in combination, may lead to negative BEF relationships. For example, metabolic co-regulation among bacteria may create a negative complementarity effect if species directly interfere with each other’s ability to function, leading to a negative BEF.

To test these ideas, we built a consumer-resource model drawing inspiration from microbial communities in pitcher plants. These carnivorous plants produce modified leaves in the shape of cups and use nectar to lure insects and other animals that fall into these pit traps and drown within the accumulated fluid (Ellison, Miller). Prey represent a key source of nitrogen, phosphorus, and micronutrients for these plants, which inhabit nutrient-poor soils. While microbial communities play important roles across all pitcher plants, species such as *D. californica* and *S. purpurea* produce little to no endogenous enzymes, thus depending on their microbial communities for prey degradation and nitrogen provision. Our model combines competition for resources with a by-production metabolic network and co-regulation among microbes (Fig. 1) to investigate how different community assembly conditions lead to different BEF relationships. We are interested in (1) assessing the degree to which niche relationships, by-production architecture, co-regulation scenarios, and differences in resource quality and resource handling time influence BEF relationships, (2) determining whether complementarity or selection effects dominate the direction of the BEF (positive, negative, or null) in this system, and (3) understanding why negative BEF are rare.

# Materials and Methods

We simulate consumer-resource dynamics in the microbial community inside a pitcher plant leaf throughout the life cycle of the leaf. The leaf is initially sterile and is then colonized by bacteria, which continually disperse into the leaf at a constant rate from a species pool with 50 species. We control species richness by allowing only a subset of species pool to disperse into the leaf (seeded richness). Insects fall into the leaf and are decomposed by the bacterial community, releasing ammonia in the process (Fig. 1A). Following empirical observations (CITATION), most of the insect supply occurs early in the cycle, declining exponentially over time. The simulation encompasses the entire population dynamics within the leaf, such that by the end of the simulation, all populations have died out due to resource limitation. The total amount of ammonia produced by the end of the life of the leaf is our measure of function in this system.

Falling insects provide a set of 50 different resources to the bacteria in the pitcher. The affinities of each species for each resource define their niches. We use a type-II functional response, such that resource uptake saturates according to each species handling time. When bacteria uptake a unit of resource, three processes take place: growth, release of by-products to the media, and release of ammonia (Fig. 1B). Growth is mediated by resource quality: higher-quality resources promote more growth for the same amount of resource consumed. By-products consist of other resources which are then available to be taken up by other bacteria. Resources are arranged in a chain such that consumption of a given resource can yield only down-chain by-products. Ammonia is produced upon consumption of all resources and is not used as a resource by any species. Species are labelled numerically such that high-index species produce more ammonia per unit resource than low-index species. In addition, ammonia production can be inhibited by the presence of other bacteria (co-regulation, Fig. 1C). We examine seventeen seeded richness levels, three niche scenarios, three handling time scenarios, two resource quality scenarios, three by-production chain architectures, and four co-regulation scenarios (Fig. 1D-H, see details below), for a total of 3,672 different scenarios. Each scenario is replicated 50 times with a different random set of seeded species, for a total of 183,590 simulations (see also Table S1).

## Dynamical model

We model the dynamics of a microbial community in the pitcher plant as a resource-consumer model, where microbial strains with densities (), consume carbon-based resources with concentrations () as follows:

|  | (1a) |
| --- | --- |
|  | (1b) |

In eq. (1a), the concentration of each resource varies due to (i) influx via falling insects at a time-dependent rate assumed equal for all resources, (ii) consumption by bacteria with functional response , and (iii) production by bacteria as byproducts of consumption of other resources. The uptake rate of each resource by each species follows Michaelis-Menten kinetics:

where is the affinity of species for resource and is the handling time of species , such that gives the maximal uptake rate of the resource by species when that resource is non-limiting and uptake is instead limited by physiological constraints. Species produces resource at a per-capita rate resulting from its combined consumption of all other resources :

where is the proportion of resource consumed by species that, after being partially metabolized, leaks back into the media as resource .

In eq. (1b), the density of each microbial strain varies due to (i) immigration into the pitcher from the outer environment at a constant rate , (ii) microbial growth in the pitcher at rate as a function of resource consumption, and (iii) death through a constant mortality rate . The growth rate is jointly limited by the availability of the multiple carbon-based resources in the pitcher, which act as substitutable resources (Tilman, 1980):

Thus, the overall growth rate of species results from the additive consumption of each resource at rate , discounted by a loss through leaching out of byproducts. The latter is due to mass balance, such that only a proportion of consumed resource ends up fueling growth. Lastly the factor , associated with the quality of resource , converts metabolized resource into new bacterial growth.

We modeled the transient nature of a pitcher from its opening () to senescence () by assuming that the rate of resource input in the pitcher, which captures the fall and death of insects into it, is at its highest at the initial time and decreases exponentially with a characteristic time , i.e. . Since resource supply eventually dries out, all resources eventually disappear (), and all the microbial strains eventually go extinct () as time goes to infinity (). (In practice, we stop the simulation at , see Table S1.)

## Ammonia production

In addition, we assume that every unit of uptake by microbes also generates nitrogen-based byproducts that, for simplicity, are assumed not to be consumed by the microbes, feeding instead an ammonia pool inside the pitcher with concentration . This pool of released ammonia is the *ecosystem functioning* of our microbial community from the plant’s perspective. We do not explicitly model plant uptake from this pool, instead measuring its total accumulation throughout the lifetime of the pitcher:

This function features our last ingredient of the model, the efficiency of ammonia production . We assumed that depends on the identity of the consumer but not on the resource. In addition, we included co-regulation---microbes’ ability to suppress metabolic activity of other microbes (CITATION) --- by modeling as a function of the densities of the microbes present in the system (see scenarios below). Since the microbial community eventually goes extinct, the total amount of ammonia produced eventually converges onto a finite value.

## Simulation scenarios

The subsections below describe our simulation scenarios. For a complete list of fixed parameters and their values used in this study, see Table S1. For a summary of all simulation scenarios, see Table S2.

### Seeded richness

To study how microbial diversity affects ecosystem functioning, we mimic the classical setup of a BEF experiment by controlling the level of microbial diversity that is allowed to assemble in the pitcher through immigration (seeded richness). In practice, for each level of biodiversity chosen, we picked species from a predetermined species pool of 50 species and let them continually invade the pitcher with a small, constant immigration rate ( for these species), while the immigration rates of the remaining species were set to 0. A simulation run starts with a completely empty pitcher ( and ) at . Then, we let the community assemble as resources and bacteria flow in and we record the total amount of ammonia produced . At the end of the simulation, all microbes eventually die and stabilizes. We looked at seventeen different levels of seeded richness, 1, 3, 5, …, 19, 24, 29, 34, …, 49, 50. We replicated each diversity level 50 times by generating all possible species combinations when or , and by randomly picking a subset of the species pool when and .

### Niche scenarios

The microbial species pool contains all the possible microbial species that can be let into the pitcher, and thus needs to be generated beforehand. Species in the pool differed functionally from each other by their affinity to different resources, i.e. by the entries of the matrix. Each row of this matrix defines the niche of the respective species. We considered three different *niche scenarios* (Fig. 1D) to explore how general types of niche relationships influence the BEF relationship. Two of these scenarios relied on our hierarchical ordering of resources by their ability to yield other resources as byproducts of their metabolism, mimicking a decomposition processing chain. The niche scenarios are as follows: (i) *Generalists*, where all species consume all resources with fixed, randomly drawn affinities ; (ii) *Specialists*, where each species specializes on the resource with identical index along the processing chain, (, all other ); (iii) *Gradient*, where each species consumes its corresponding resource and all other resources down the chain. In the latter scenario, up-chain species can use more resources than down-chain species. We offset this competitive advantage by standardizing the row-sums of the matrix, so that the specialized down-chain species have the same total uptake ability as the generalist up-chain species ( if , all other ).

### By-production architecture

We test the influence of cross-feeding on BEF relationships by examining three *by-production architecture* scenarios (Fig. 1E): (i) *Serial by-production*, where consumption of resource yields only resource as a by-product (we set for all , and all other ); (ii) *Nested by-production*, where consumption of resource yields all down-chain resources (we set for & , and otherwise. This gives the nested architecture while standardizing all row-sums to); (iii) *No by-production,* where all .

### Handling time scenarios

Competitive dynamics depend not only on species niches but also their ability to quickly deplete resources. Species able to quickly process resources can have a competitive advantage over those with longer handling times. We examine the degree to which species differences in this timing affect BEF relationships by comparing three handling time scenarios (Fig. 1F): (i) *Flat*, where is the same for all species (), (ii) *Increase*, where down-chain species have higher handling time. Here, we set , such that handling time increases exponentially down the species chain from to ; (iii) *Decrease*, where down-chain species have lower handling time. Here, we set , such that handling time decreases exponentially down the species chain from to .

### Resource quality scenarios

If some resources fuel more growth per unit consumed than others, then species that specialize in those resources may dominate the community, possibly leading to selection effects in ecosystem functioning. We test this hypothesis by considering two *resource quality scenarios* (Fig. 1G): (i) *Flat*, where all resources support the same microbial growth per unit consumed (); (ii) In*crease*, where down-chain resources support higher microbial growth. This represents a scenario where down-chain resources are simpler, less recalcitrant molecules, which are easier to break down and therefore provide higher growth efficiency. Here, we arbitrarily defined , which is a convex increasing function of with and ). We did not consider the opposite resource quality scenario for lack of a biological justification and because preliminary results indicated that differences in resource quality had little effect on the BEF relationships (see Results).

### Co-regulation scenarios

Finally, we investigated the role played by species interactions on ammonia production that are not mediated by resources. We modeled metabolic co-regulation among bacteria (CITATION) assuming exponential density-dependence:

Where the constant parameter captures the intrinsic ammonia production rate of species . We set , such that species at the top of the chain have higher ammonia production capacity than those at the bottom. This reflects an assumed hierarchy among species in their investment in producing the enzymes that metabolize nitrogen. In the Specialists niche scenario, the strongest ammonia producers specialize in resources near the top of the chain (e.g., the larger molecules); in the Gradients niche scenario, the strongest ammonia producers are generalists while the weak producers are bottom-chain resource specialists.

The exponential factor captures the fact that overall microbial density inhibits ammonia production, with pairwise exponents quantifying the degree to which species inhibits ammonia production by species . We focused on four *co-regulation scenarios* (Fig. 1H): (i) *Absent*, where there was no inhibition (); (ii) *Neutral*, where all species inhibited each other equally, i.e. ; (iii) *Interspecific*, where interspecific inhibition is greater than intraspecific inhibition, i.e. for ; (iv) *Intraspecific*, where intraspecific inhibition is greater than interspecific inhibition, i.e. for .

## Analysis

### Complementarity and selection effects

Once one accounts for total community size, a positive or negative BEF can only occur if species perform differently in mixture than in monoculture. If that occurs, then the total function in a multispecies community will deviate from the sum of the function produced by each species in isolation. Furthermore, any such differences in function will result from the combined effect of complementarity and selection. Following (CITATION), we calculate complementarity in a community with seeded species using the formula:

where is the amount of ammonia produced by species in monoculture and is the difference between the amount of ammonia that species produced in mixture and what it would produce in monoculture given the same relative abundance. This expression will be positive if species produce more ammonia on average when in mixture than when alone, and it will be negative when the reverse is true.

We calculate selection using the formula:

That is, the selection effect results from a correlation between the amount of ammonia a species produces in mixture and the amount it produces in monoculture. It will be positive if species with high ammonia production capacity tend to dominate mixtures, and it will be negative if the reverse is true.

### Importance of model scenarios on the shape of the BEF relationship

We kept a record of the shapes of BEF relationships (i.e., null, negative, positive, unimodal) observed across the cross-factorial combination of model scenarios (i.e., niche scenario, co-regulation scenario, resource quality, handling time, and by-production architecture). We then used these data to fit a classification random forest that allowed us to identify the chief determinants of these shapes. Random forests are useful for identifying patterns in data because they do not assume any relationship between the response (here, BEF shape) and predictors (here, model scenarios), and automatically model the effect of interactions among predictors on the response (Breiman 2001). Consequently, they are often used in analyses of data generated through complex and interactive simulation designs that aim at identifying the main drivers of variation in ecological systems (e.g., Guzman et al. 2022, O’Sullivan et al. 2023).

To fit the classification random forest, we started by creating 1,000 bootstrap samples from the original data. For each of these samples, we fit classification trees that used a small random subset of predictors (here, 3) to split the bootstrapped data into groups corresponding to different BEF shapes. We used the generated classification trees to predict the BEF shape of out-of-bag (OOB) observations (i.e., the part of the original data not used in the bootstrapped samples). The predicted BEF shape of a given OOB observation was determined by the majority vote across trees. The predictive ability of the random forest classifier was then estimated based on the proportion of the OOB observations that were incorrectly classified (i.e., the OOB error rate). The importance of predictors in the random forest is determined by the increase in OOB error rate when a given predictor is permuted while keeping the remaining predictors intact (Breiman 2001). We followed Ishwaran and Lu (2019) to estimate variation in the measurements of predictor importance through a combination of bootstrapping and subsampling.

We conducted the random forest modeling pipeline using the randomForestSRC package (Ishwaran and Kogalur 2023) in R version 4.2.2.

# Results

In all simulated scenarios, the number of microbial species that achieved a measurable population size inside the leaf tracked the number of species allowed to colonize it (Fig. S1). This indicates that seeded richness is a good indicator of realized richness, and hence that the measured relationship between total ammonia production and seeded richness was a reliable proxy for BEF relationships inside the leaf.

We observed several qualitatively different shapes of the BEF relationship across our model scenarios (Fig. 2), with fully negative BEF relationships occurring in only a small minority of scenarios. Here, we momentarily focus on scenarios with nested by-production network architecture and identical handling time across species for the sake of example. In Fig. 2, datapoints show the total amount of ammonia produced in the leaf in 50 replicates of each seeded richness level, while black curves show averages. In scenarios where all resources have the same quality (Flat resource quality scenario, Fig. 2a), the BEF relationship was null, positive, or negative in the Generalists niche scenario (left column) depending on the co-regulation scenario (rows); the BEF was always positive in the Specialists niche scenario (center column); it was positive or modal (i.e., increasing at low richness and decreasing at high richness) in the Gradients scenario depending on co-regulation. Results were similar in scenarios with increasing resource quality down the resource chain (Increase resource quality scenario, Fig. 2b), except that the Specialists niche scenario showed a modal BEF relationship when co-regulation occurred.

Overall, the BEF relationship had a negative component only when co-regulation was present, and especially when co-regulation across species was stronger than within species (bottom row in Fig. 2). And even then, only in the Generalists scenario was function in mixed communities lower than in the average monoculture (i.e., fully negative BEF, bottom-left panels in Fig. 2a, 2b). In the other niche scenarios, function in mixed communities was always higher than in monocultures, and only showed a negative relationship with richness at high richness levels. We note that in most scenarios, total function varied widely across replicates of a given richness level, indicating a strong effect of species composition on total function.

In our other model scenarios, the shape of the BEF relationship largely resembled their analogues in those shown in Fig. 2. Fig. 3 shows the BEF under alternative scenarios of handling time (line color) and by-production architecture (line type) while focusing on scenarios with identical resource quality for all resources (see Fig. S?? for scenarios where resource quality increases down the resource chain). Curves show averages across replicates, with datapoints removed for visual clarity. While in these scenarios the total function in the pitcher (curve height) and the strength of dependence of function on species richness (curve steepness) differed from their Fig. 2a analogues (shown as the dotted green lines in Fig. 3), the shape of the BEF relationship was similar.

However, the handling time relationships across species critically affected the shape of the BEF in the Generalists niche scenario. Specifically, the BEF relationship was negative when handling time decreased down the species chain (left column, red curves in Fig. 3), positive or modal when handling time increased down the species chain (blue curves), and null, positive, or negative when handling time was identical across species (green curves). These shapes were further modulated by co-regulation, tending towards more negative BEF relationships when co-regulation was stronger across species and more positive relationships when co-regulation was stronger within species.

The magnitude and direction of the complementarity effect varied substantially across niche and co-regulation scenarios (Fig. 4), both in absolute terms and relative to the selection effect. The complementarity effect was always positive in the Specialists scenario, where niche differentiation is maximal. In both the Generalists and Gradient niche scenarios, the direction of the complementarity effect depended on co-regulation (being negative only under strong interspecific co-regulation) while its magnitude was also affected by the by-production architecture (being weakest under no by-production and strongest under serial by-production).

In all three niche scenarios, the direction of the selection effect depended on handling time relationships, tending to be negative when species with higher ammonia capacity had higher handling times (Decrease scenario, red datapoints in Fig. 4), but positive or small otherwise. As with complementarity, the magnitude of the selection effect was further influenced by the by-production architecture, being weakest under no by-production and strongest under serial by-production. Co-regulation had no discernible influence on the selection effect.

Generally speaking, the complementarity effect dominated the Specialists niche scenario (where niche differentiation was maximal), selection dominated the Generalists niche scenario (where niche differentiation was minimal), and both effects were roughly evenly matched in the Gradient scenario (where niche differentiation was intermediate).

In scenarios with equal resource quality across resources (Fig. 3, 4), both the complementarity effect and the selection effect were often positive or negligible, and the BEF relationships were accordingly positive or null. In scenarios where the BEF was modal, complementarity and selection had opposite signs (second and fourth quadrants in Fig. 4). Scenarios where resource quality increased down the resource chain showed similar behavior, except for modal BEF relationships in the Specialists scenario despite positive complementarity and negligible selection (Fig. S2, S3). The latter was caused by a drop in complementarity at high richness in that scenario (Fig. S4), which in turn was due to a strong, negative impact of a few species on ammonia production (Fig. S5).

Complementarity had an edge over selection on influencing the BEF shape. The BEF was positive in scenarios with strongly positive complementarity even if selection was negative (Gradient niche scenarios under the Decrease handling time scenario, compare red lines and shapes in the rightmost panels in Fig. 3, 4, S2, S3). In the only scenarios where the BEF relationship was fully negative, complementarity was either negative (which occurred when co-regulation was strong across species), or negligible against a negative selection effect (which occurred in the Generalists scenario with Absent or Neutral co-regulation and under the Decrease handling time scenario).

Visual inspection of Fig. 3, S2 suggests that niche relationships and co-regulation were the most important determinants of BEF shape; handling time also had a strong influence, albeit mostly in the Gradients niche scenario, whereas resource quality and by-production architecture had comparatively minor influence. This is confirmed by the random forest classifier, which identified niche relationships as the single best predictor of BEF shape, followed by handling time, co-regulation, resource quality, and by-production architecture (Fig. 5). The out-of-bag error rate was 6.5%, indicating high classification accuracy (see confusion matrix in Table S3 and the list of BEF shapes for all simulated scenarios in Table S4). Surprisingly, by-production architecture had negative importance, meaning that the classifier was more accurate in predicting the BEF shape when ignoring that information.

# Discussion

Biodiversity-ecosystem function relationships differed greatly across our model scenarios, but were usually positive, modal, or null. A negative relationship occurred only when species directly interfered with one another’s ability to produce ammonia, causing a negative complementarity effect, or when species with lower ammonia production capacity were more competitive than high ammonia yielders due to having lower handling times, causing a negative selection effect. In all other circumstances, higher species diversity led to higher function. Furthermore, the only niche scenario where function in mixed communities was lower than in the average monoculture was the Generalists case, wherein all species shared all resources. In scenarios with stronger niche differentiation (Specialists and Gradient niche scenarios), function never decreased from monoculture to low-richness mixed cultures; in the Specialists scenarios, a negative BEF was only possible at high richness levels.

The high degree of variation in total function for a given seeded richness across replicates of the same scenario would make it difficult to detect a significant trend in diversity-function relationships without access to many such replicates. In addition, gains in function often had diminishing returns with further increases in richness, sometimes quickly asymptoting at intermediate to high richness levels. Since empirical studies are usually constrained by sample size and range of observed richness, these limitations may partially explain why null biodiversity-function relationships are common in the literature.

The complementarity effect had an overall stronger influence on the shape of the BEF than the selection effect. This is not to say that the selection effect failed to contribute to the BEF shape. For example, in the Generalists and Gradient niche scenarios where complementarity was negative due to interspecific co-regulation, (Fig.4, bottom-row panels), the selection effect was sufficiently positive to outweigh the negative complementarity and cause a function surplus relative to monoculture at low richness (Fig. 3, S2). However, the selection effect in those scenarios was largely independent of richness, while complementarity had a strongly negative relationship with richness, thus creating the negative relationship between function and richness at intermediate to high richness levels. In other words, while both complementarity and selection effects contributed to the differences in function in species mixtures relative to monoculture, the complementarity effect often drove the relationship between function and richness because of its stronger sensitivity to changes in richness levels. This could be partly because the selection effect quickly saturates once very high-yielding or low-yielding species are already sampled, whereas no such constraint applies to the complementarity effect.

Our finding that negative BEF relationships occurred in only a minority of our model scenarios mirrors their relative uncommonness in the empirical literature. Our results suggest that negative BEF relationships in nature are likely to occur in communities composed of niche-overlapping species which directly interfere with one another’s ability to yield function beyond the effects of competition for resources. In those communities, the complementarity effect may be negative, such that species on average yield less function in mixture than in monoculture. In addition, communities with low niche differentiation where strong competitors yield low function will likely face a negative selection effect. SAY SOMETHING ABOUT IT BEING UNKNOWN OR UNKNOWABLE HOW OFTEN EACH OF OUR SCENARIOS WILL OCCUR IN NATURE.

While all dimensions of variation in our model scenarios influenced the quantitative association between species diversity and function, niche relationships and co-regulation (which modulated the complementarity effect) and handling time (which modulated the selection effect) were much stronger predictors of its overall shape than resource quality and the presence and nature of cross feeding. The relative independence of the BEF shape on factors beyond niche partitioning, competitive hierarchies, and direct interference suggests that our results generalize to communities beyond microbes in pitcher plants to any multispecies communities where function is a direct outcome of resource consumption.

In fact, the strong connection between the shape of the BEF and niche relationships is in part due to function in our model being a direct consequence of resource consumption. When species niche-differentiate by partitioning resources, a positive relationship between species diversity and function becomes almost inevitable. Here, it was only possible to break this positive relationship when function was detached from resource consumption via direct co-regulation on ammonia production, or when we manually inserted a negative relationship between species competitive ability and ammonia production capacity. Other types of function such as XXX, which are less tightly connected to resource consumption, may be less tied to niche relationships.

While in our model co-regulation had no impact on growth, in nature the release of secondary metabolites to shared media often affects the growth of other species by slowing down their resource uptake. Such an association may cause selection effects if strong regulators are also strong competitors for resources. Future work should examine whether this may have a qualitative impact on the shape of the BEF, overpowering the contribution of the complementarity effect. While our model did not examine predation, bacterivore TYPES OF ORGANISMS might influence the BEF relationship, because preferential predation of species with high ammonia output may cause strong selection effects. Finally, we assumed that species have equal dispersal ability and colonize pitchers at equal rates. However, this assumption may be violated by commensal bacteria arriving with the insects that fall in, or by bacteria with particularly motile spores. Such differences in propagule rain may affect competitive outcomes and could potentially impact BEF relationships.

MORE PARAGRAPHS DISCUSSING HOW OUR RESULTS CONNECT WITH LITERATURE, preferably referencing Box 1.

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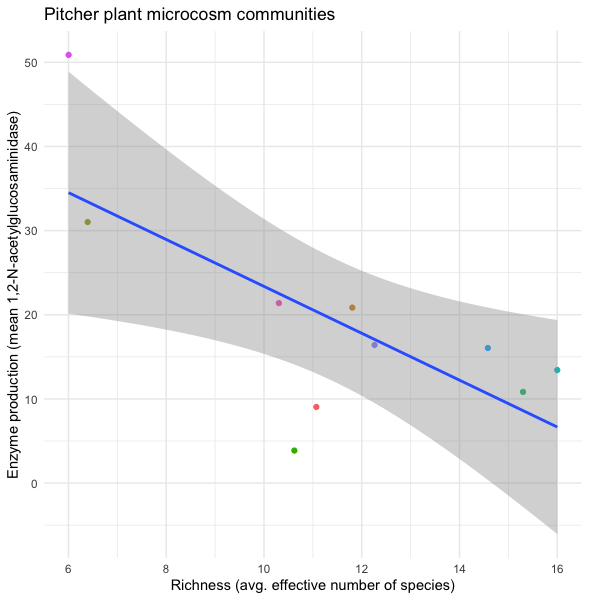
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# Box 1

Negative BEF relationships are rare in the literature (von der Plas 2019, CITATIONS). Here, we present two examples of negative BEF patterns that may be driven by similar mechanisms as shown in this study, such as interspecific and intraspecific co-regulation of enzyme activity. We define function in the context of nutrient cycling, where living organisms contribute to transformations of energy and matter. Two biogeochemical cycles central to this discussion are those of carbon and nitrogen, particularly as they relate to microbial activity.

Our first example of a negative BEF relationship is in a wastewater treatment system, an environment with high nitrogen input. [Context, sampling design, results, and figure here].

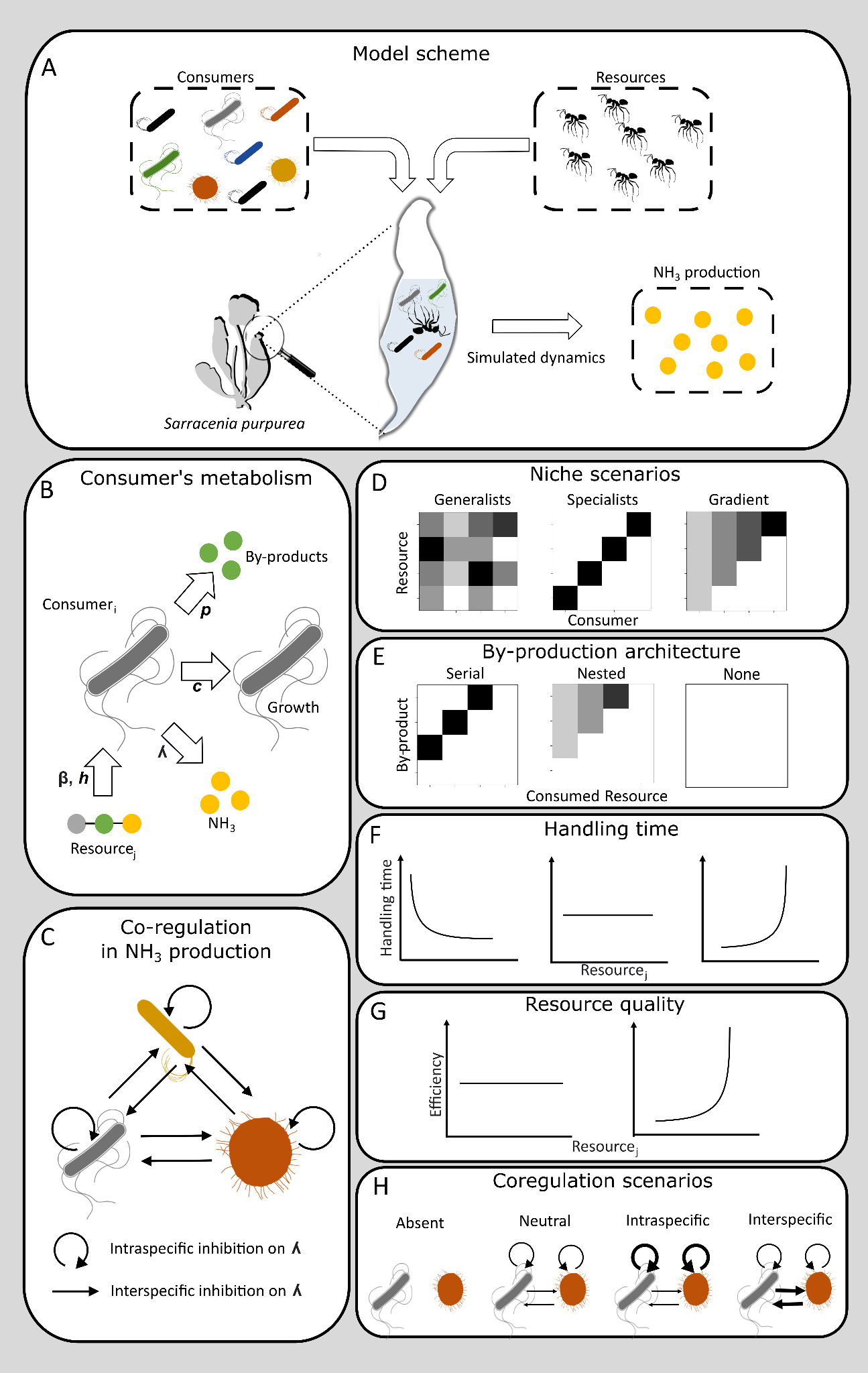
Our second example of a negative BEF relationship is enzyme production in *Sarracenia purpurea* pitcher plant microcosms. Pitcher plants capture and digest insects to access essential nutrients such as nitrogen, and chitin is the main biopolymer of the insect exoskeleton. Thus, we regard the extracellular production of chitinase enzymes by the contained microbial community as a key ecosystem function. The data were gathered as part of an experiment investigating how assembly history affected re-assembly and community function in a controlled laboratory environment [ref Bittleston et al paper]. Samples of pitcher fluid were collected from the natural habitat in Massachusetts and grown in deepwell plates with acidified cricket media in a growth chamber. Community cultures were moved to new media every 3 days in a 1:1 ratio, and with each transfer, samples were taken for enzyme assays and 16S rRNA metabarcoding. The communities were found to equilibrate after about 3 weeks (21 transfers). Here, we reanalyze the data in a BEF framework to examine how community production of the enzyme N-acetyl-β-d-glucosaminidase changed with species richness, measured as the effective number of species in the community (the exponential of the Shannon diversity, or Hill number of order 1). This enzyme cleaves N-acetyl-glucosamine monomers from chitin molecules (i.e., chitobiose, chitotriose), breaking the oligosaccharides into smaller units. From this new analysis, we find that communities with higher biodiversity have lower enzyme production, leading to a negative BEF relationship (Box Figure 2).



**Box Figure 2**. Ecosystem function, measured as average enzyme production in equilibrated laboratory microcosm communities, decreases with increasing species richness, measured as the average effective number of species (exponent of the Shannon diversity).

## 

# Figures



**Figure 1. Schematic representation of our model, the processes in the pitcher plant microbial community, and the model scenarios examined in this study.**

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Description automatically generated Figure 2. BEF shapes were variously positive, negative, null, or modal.** Data points represent total cumulative ammonia production by the end of the simulation for each simulation. Each richness level is replicated 50 times with a random sampling of the species pool being seeded into the pitcher. Black curves show the average function at each richness level. Columns show niche scenarios, row show co-regulation scenarios. **a**. Resource quality is identical for all resources. **b**. Resource quality increases down the resource chain. The Specialists scenario shows a bifurcation at n = 44 when co-regulation was present (see Fig. S4, S5 for more details). All simulations had nested by-production network and identical handling times across species.

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Description automatically generated Figure 3. BEF relationships in alternative scenarios of handling time and by-production architecture**. Curves show the function at each richness level averaged across 50 replicates. Columns show niche scenarios, rows show co-regulation scenarios. Line color represents the handling time scenario, line type represents the by-production architecture. Resource quality is identical across resources.

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**Figure 4. Complementarity and selection effects in our model scenarios**. Each data point shows complementarity and selection effects averaged across richness levels for the corresponding scenario in Fig. 3. Handling time scenarios and by-production architecture scenarios are represented by colors and shapes, respectively. Axes are cube-rooted to ease visualization.

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**Figure 5. Importance of each dimension of variation in our model as a determinant of BEF shape.**  Variable importance was determined by a random forest algorithm, given by the percentage increase in out-of-bag error rates when the focal predictor is permuted while the remaining predictors are kept fixed. Variation in the estimates of variable importance were obtained through a combination of bootstrapping and subsampling. Boxplots show median and interquartile ranges.

# Supplementary Figures

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**Figure S1. Realized species richness tracks seeded richness.** Realized richness increased in proportion to seeded richness in all simulation scenarios. Realized richness was calculated as the maximum number of species with concurrent population size above the 75th quantile of all population sizes observed throughout the simulation. Although lower thresholds led to higher slopes, the collinearity was robust to the choice of quantile threshold. Grey lines show the one-to-one relationship.

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**Figure S2. BEF relationships for simulation scenarios with increasing resource quality down the resource chan.** BEF shapes are similar to corresponding scenarios with flat resource quality (compare with Fig. 3 in the main text), except for modal shapes in the Specialists niche scenario.

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**Figure S3. Complementarity and selection effects across simulations with increasing resource quality down the resource chain.** Plots are arranged as in Fig. 4 in the main text. As withscenarios with identical resource quality across resources (compare Fig. 4 in the main text), niche relationships and co-regulation had a stronger influence on the magnitude and direction of both effects than handling time and by-production architecture, with some exceptions. The complementarity effect is always positive in the Specialists scenario (where niche differentiation is maximal), but close to zero in the Generalists scenario (where niche differentiation is minimal), and also usually small in the Gradient niche scenario. The selection effect on the latter two niche scenarios tends to be negative when species with higher ammonia capacity have higher handling times (Decrease scenario, red datapoints), and positive or near zero otherwise. By-production architecture typically had little influence on either effect, except in the Generalist and Gradient scenarios without co-regulations. The only cases with negative complementarity were those under strong interspecific co-regulation. Axes are cube-rooted to ease visualization.

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**Figure S4. Trends in complementarity and selection effects against seeded richness in Fig. 2 scenarios.** Blue curves: complementarity. Red curves: selection. Black curves: difference in function from monoculture (Function = Complementarity + Selection). Rows: co-regulation scenarios; columns: niche scenarios. When complementarity or selection is negligible, the other effect drives the difference in function from monoculture, and thus the BEF shape. Both complementarity and selection are approximately zero in the Generalists niche scenario under absent and neutral co-regulation, leading to a null BEF relationship. **a.** Resource quality is identical for all resources. **b.** Resource quality increases down the resource chain. The mode in the Specialists scenario is caused by a corresponding drop in complementarity. All simulations had nested by-production network and identical handling times across species.

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**Figure S5. Comparing total function in the Specialists niche scenario in replicates where species 49 and 50 were present vs absent**. **Left:** Simulations with 44 seeded species. Points lined up on the x-axis show all replicates with the respective species missing. Ecosystem function was clearly higher in replicates where Species 50 was absent (red fill) than in replicates where it was present (blue fill). Within the red and blue groups, function was higher in replicates where Species 49 was absent (square shapes) than in replicates where it was present (triangles). **Right:** Simulations with 49 seeded species. Replicates are arranged by which of the 50 species was missing. We see a clear gap in function between the replicate where Species 50 was absent and those where it was present. A smaller gap is seen between the replicate without Species 49 and those with it. These results indicate a strong negative influence of high-index species on total function. The mode in the Specialists scenario seen in Fig. 2, 3, S3, S4 is due to a split in total function at n = 44: the total amount of function bifurcated to low values when high-index species were present and high values when they were absent. The former scenarios, being more common than the latter, bent the BEF curve downwards, causing the mode. All simulations had increasing resource quality down the resource chain, nested by-production network, identical handling times across species, and no co-regulation.

# Supplementary Tables

**Table S1**. Fixed parameters used in this study.

| Parameter | Description | Value |
| --- | --- | --- |
|  | number of species in the pool | 50 |
|  | number of resources | 50 |
|  | simulation stopping time | 1000 |
|  | maximum resource supply rate | 2 |
|  | resource supply characteristic time | 1 |
|  | immigration rate | 10-17 |
|  | death rate | 0.01 |
|  | maximum resource affinity | 10 |
|  | by-production constant | 0.7 |
|  | minimum handling time | 1 |
|  | maximum handling time | 8 |
|  | minimum conversion constant | 0.8 |
|  | maximum conversion constant | 8 |
|  | minimum ammonia production constant | 1 |
|  | maximum ammonia production constant | 10 |
|  | minimum co-regulation constant | 0.05 |
|  | maximum co-regulation constant | 0.1 |

**Table S2.** Simulation scenarios examined in this study.

| **Dimension of variation / Simulation scenario** | | | **Description** | **Parameterization** |
| --- | --- | --- | --- | --- |
| 1 | Seeded richness | |  |  |
|  |  |  | randomly drawn species are seeded into the pitcher plant at the start of the simulation run, for up to a maximum of 50 species. | 1, 3, 5, …, 19, 24, 29, 34, 39, ... 50 |
| 2 | Niches | |  |  |
|  |  | Generalists | All species consume all resources with fixed, randomly drawn affinities. |  |
|  |  | Specialists | Species only consumes its corresponding resource . Thus species 1 only consumes resource 1, species 2 only consumes resource 2, etc. | all other |
|  |  | Gradient | Each species only consumes resources down-chain of itself: species 1 consumes all resources, species 2 consumes resources 2 and up, etc. The sum of resource affinities across all resources is standardized for all species. | if all other |
| 3 | By-production architecture | |  |  |
|  |  | Serial | Consumption of resource yields only resource as a by-product | for all  all other |
|  |  | Nested | Consumption of resource yields all down-chain resources . | for &  all other |
|  |  | None | No by-production. |  |
| 4 | Handling time | |  |  |
|  |  | Flat | All consumers have the same handling time. |  |
|  |  | Increase | Down-chain species have higher handling time. |  |
|  |  | Decrease | Down-chain species have lower handling time. |  |
| 5 | Resource quality | |  |  |
|  |  | Flat | All resources support the same microbial growth per unit consumed. |  |
|  |  | Increase | Down-chain resources support higher microbial growth. |  |
| 6 | Co-regulation | | |  |
|  |  | Absent | Species have no mutual influence on ammonia production. |  |
|  |  | Neutral | Inhibition of ammonia production is the same across all species. |  |
|  |  | Intraspecific | Intraspecific inhibition is greater than interspecific inhibition. |  |
|  |  | Interspecific | Interspecific inhibition is greater than intraspecific inhibition. |  |

**Table S3.** Confusion matrix for random forest classifier.

|  |  | Observed BEF shape | | | |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | Negative | Null | Positive | Modal | **Classification Error** |
| Predicted BEF shape | Negative | 43 | 0 | 1 | 0 | 0.02 |
| Null | 0 | 18 | 0 | 2 | 0.10 |
| Positive | 0 | 0 | 98 | 5 | 0.05 |
| Modal | 0 | 1 | 5 | 44 | 0.12 |

**Table S4**. Shape of BEF relationship for all simulated scenarios. Legend: positive (+), negative (-), modal (+-), null (0). The BEF was assigned a modal shape if peak function occurred neither at n = 1 nor n = 50. It was assigned a null shape if the coefficient of variation of function across seeded richness levels was below 0.03, which was empirically observed to sharply separate them from BEF relationships with a clear trend.

| Niches | Co-regulation | Handling time | Resource quality | By-production | BEF shape |
| --- | --- | --- | --- | --- | --- |
| Generalists | Absent | Decrease | Flat | None | - |
| Generalists | Absent | Decrease | Flat | Nested | - |
| Generalists | Absent | Decrease | Flat | Serial | - |
| Generalists | Absent | Decrease | Increase | None | - |
| Generalists | Absent | Decrease | Increase | Nested | - |
| Generalists | Absent | Decrease | Increase | Serial | - |
| Generalists | Absent | Flat | Flat | None | 0 |
| Generalists | Absent | Flat | Flat | Nested | 0 |
| Generalists | Absent | Flat | Flat | Serial | 0 |
| Generalists | Absent | Flat | Increase | None | 0 |
| Generalists | Absent | Flat | Increase | Nested | 0 |
| Generalists | Absent | Flat | Increase | Serial | 0 |
| Generalists | Absent | Increase | Flat | None | +- |
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| Generalists | Absent | Increase | Increase | None | + |
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| Generalists | Absent | Increase | Increase | Serial | + |
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| Generalists | Neutral | Decrease | Flat | Nested | - |
| Generalists | Neutral | Decrease | Flat | Serial | - |
| Generalists | Neutral | Decrease | Increase | None | - |
| Generalists | Neutral | Decrease | Increase | Nested | - |
| Generalists | Neutral | Decrease | Increase | Serial | - |
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| Specialists | Absent | Increase | Increase | Serial | + |
| Specialists | Neutral | Decrease | Flat | None | + |
| Specialists | Neutral | Decrease | Flat | Nested | + |
| Specialists | Neutral | Decrease | Flat | Serial | + |
| Specialists | Neutral | Decrease | Increase | None | +- |
| Specialists | Neutral | Decrease | Increase | Nested | +- |
| Specialists | Neutral | Decrease | Increase | Serial | + |
| Specialists | Neutral | Flat | Flat | None | + |
| Specialists | Neutral | Flat | Flat | Nested | + |
| Specialists | Neutral | Flat | Flat | Serial | + |
| Specialists | Neutral | Flat | Increase | None | +- |
| Specialists | Neutral | Flat | Increase | Nested | +- |
| Specialists | Neutral | Flat | Increase | Serial | + |
| Specialists | Neutral | Increase | Flat | None | + |
| Specialists | Neutral | Increase | Flat | Nested | + |
| Specialists | Neutral | Increase | Flat | Serial | + |
| Specialists | Neutral | Increase | Increase | None | +- |
| Specialists | Neutral | Increase | Increase | Nested | +- |
| Specialists | Neutral | Increase | Increase | Serial | +- |
| Specialists | Intraspecific | Decrease | Flat | None | + |
| Specialists | Intraspecific | Decrease | Flat | Nested | + |
| Specialists | Intraspecific | Decrease | Flat | Serial | + |
| Specialists | Intraspecific | Decrease | Increase | None | + |
| Specialists | Intraspecific | Decrease | Increase | Nested | +- |
| Specialists | Intraspecific | Decrease | Increase | Serial | + |
| Specialists | Intraspecific | Flat | Flat | None | + |
| Specialists | Intraspecific | Flat | Flat | Nested | + |
| Specialists | Intraspecific | Flat | Flat | Serial | + |
| Specialists | Intraspecific | Flat | Increase | None | +- |
| Specialists | Intraspecific | Flat | Increase | Nested | +- |
| Specialists | Intraspecific | Flat | Increase | Serial | + |
| Specialists | Intraspecific | Increase | Flat | None | + |
| Specialists | Intraspecific | Increase | Flat | Nested | + |
| Specialists | Intraspecific | Increase | Flat | Serial | + |
| Specialists | Intraspecific | Increase | Increase | None | +- |
| Specialists | Intraspecific | Increase | Increase | Nested | +- |
| Specialists | Intraspecific | Increase | Increase | Serial | +- |
| Specialists | Interspecific | Decrease | Flat | None | + |
| Specialists | Interspecific | Decrease | Flat | Nested | + |
| Specialists | Interspecific | Decrease | Flat | Serial | + |
| Specialists | Interspecific | Decrease | Increase | None | +- |
| Specialists | Interspecific | Decrease | Increase | Nested | +- |
| Specialists | Interspecific | Decrease | Increase | Serial | + |
| Specialists | Interspecific | Flat | Flat | None | + |
| Specialists | Interspecific | Flat | Flat | Nested | + |
| Specialists | Interspecific | Flat | Flat | Serial | + |
| Specialists | Interspecific | Flat | Increase | None | +- |
| Specialists | Interspecific | Flat | Increase | Nested | +- |
| Specialists | Interspecific | Flat | Increase | Serial | + |
| Specialists | Interspecific | Increase | Flat | None | + |
| Specialists | Interspecific | Increase | Flat | Nested | + |
| Specialists | Interspecific | Increase | Flat | Serial | + |
| Specialists | Interspecific | Increase | Increase | None | +- |
| Specialists | Interspecific | Increase | Increase | Nested | +- |
| Specialists | Interspecific | Increase | Increase | Serial | +- |
| Gradient | Absent | Decrease | Flat | None | + |
| Gradient | Absent | Decrease | Flat | Nested | + |
| Gradient | Absent | Decrease | Flat | Serial | + |
| Gradient | Absent | Decrease | Increase | None | 0 |
| Gradient | Absent | Decrease | Increase | Nested | 0 |
| Gradient | Absent | Decrease | Increase | Serial | 0 |
| Gradient | Absent | Flat | Flat | None | + |
| Gradient | Absent | Flat | Flat | Nested | + |
| Gradient | Absent | Flat | Flat | Serial | + |
| Gradient | Absent | Flat | Increase | None | + |
| Gradient | Absent | Flat | Increase | Nested | + |
| Gradient | Absent | Flat | Increase | Serial | + |
| Gradient | Absent | Increase | Flat | None | + |
| Gradient | Absent | Increase | Flat | Nested | + |
| Gradient | Absent | Increase | Flat | Serial | + |
| Gradient | Absent | Increase | Increase | None | + |
| Gradient | Absent | Increase | Increase | Nested | + |
| Gradient | Absent | Increase | Increase | Serial | + |
| Gradient | Neutral | Decrease | Flat | None | 0 |
| Gradient | Neutral | Decrease | Flat | Nested | 0 |
| Gradient | Neutral | Decrease | Flat | Serial | 0 |
| Gradient | Neutral | Decrease | Increase | None | - |
| Gradient | Neutral | Decrease | Increase | Nested | - |
| Gradient | Neutral | Decrease | Increase | Serial | - |
| Gradient | Neutral | Flat | Flat | None | + |
| Gradient | Neutral | Flat | Flat | Nested | + |
| Gradient | Neutral | Flat | Flat | Serial | + |
| Gradient | Neutral | Flat | Increase | None | +- |
| Gradient | Neutral | Flat | Increase | Nested | + |
| Gradient | Neutral | Flat | Increase | Serial | +- |
| Gradient | Neutral | Increase | Flat | None | + |
| Gradient | Neutral | Increase | Flat | Nested | + |
| Gradient | Neutral | Increase | Flat | Serial | + |
| Gradient | Neutral | Increase | Increase | None | + |
| Gradient | Neutral | Increase | Increase | Nested | + |
| Gradient | Neutral | Increase | Increase | Serial | + |
| Gradient | Intraspecific | Decrease | Flat | None | + |
| Gradient | Intraspecific | Decrease | Flat | Nested | + |
| Gradient | Intraspecific | Decrease | Flat | Serial | + |
| Gradient | Intraspecific | Decrease | Increase | None | + |
| Gradient | Intraspecific | Decrease | Increase | Nested | - |
| Gradient | Intraspecific | Decrease | Increase | Serial | + |
| Gradient | Intraspecific | Flat | Flat | None | + |
| Gradient | Intraspecific | Flat | Flat | Nested | + |
| Gradient | Intraspecific | Flat | Flat | Serial | + |
| Gradient | Intraspecific | Flat | Increase | None | + |
| Gradient | Intraspecific | Flat | Increase | Nested | + |
| Gradient | Intraspecific | Flat | Increase | Serial | + |
| Gradient | Intraspecific | Increase | Flat | None | + |
| Gradient | Intraspecific | Increase | Flat | Nested | + |
| Gradient | Intraspecific | Increase | Flat | Serial | + |
| Gradient | Intraspecific | Increase | Increase | None | + |
| Gradient | Intraspecific | Increase | Increase | Nested | + |
| Gradient | Intraspecific | Increase | Increase | Serial | + |
| Gradient | Interspecific | Decrease | Flat | None | - |
| Gradient | Interspecific | Decrease | Flat | Nested | - |
| Gradient | Interspecific | Decrease | Flat | Serial | - |
| Gradient | Interspecific | Decrease | Increase | None | - |
| Gradient | Interspecific | Decrease | Increase | Nested | - |
| Gradient | Interspecific | Decrease | Increase | Serial | - |
| Gradient | Interspecific | Flat | Flat | None | +- |
| Gradient | Interspecific | Flat | Flat | Nested | +- |
| Gradient | Interspecific | Flat | Flat | Serial | +- |
| Gradient | Interspecific | Flat | Increase | None | - |
| Gradient | Interspecific | Flat | Increase | Nested | - |
| Gradient | Interspecific | Flat | Increase | Serial | - |
| Gradient | Interspecific | Increase | Flat | None | +- |
| Gradient | Interspecific | Increase | Flat | Nested | +- |
| Gradient | Interspecific | Increase | Flat | Serial | +- |
| Gradient | Interspecific | Increase | Increase | None | +- |
| Gradient | Interspecific | Increase | Increase | Nested | +- |
| Gradient | Interspecific | Increase | Increase | Serial | +- |