Assembly Graph as the Rosetta Stone of Ecological Assembly

Integrating Dynamical, Informational, and Probabilistic Perspectives

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Abstract

Ecological assembly—the process of ecological community formation through species introductions—has recently seen exciting theoretical advancements across dynamical, informational, and probabilistic approaches. However, these theories often remain inaccessible to non-theoreticians, and they lack a unifying lens. Here, I introduce the assembly graph as an integrative tool to connect these emerging theories. The assembly graph visually represents assembly dynamics, where nodes symbolize species combinations and edges represent transitions driven by species introductions. Through the lens of assembly graphs, I review how ecological processes reduce uncertainty in random species arrivals (informational approach), identify graphical properties that guarantee species coexistence and examine how the class of dynamical models constrain the topology of assembly graphs (dynamical approach), and quantify transition probabilities with incomplete information (probabilistic approach). To facilitate empirical testing, I also review methods to decompose complex assembly graphs into smaller, measurable components, as well as computational tools for deriving empirical assembly graphs. In sum, this math-light review of theoretical progress aims to catalyze empirical research towards a predictive understanding of ecological assembly.

> The concept […] is to create order out of chaos based on random drawing of tiles.
>
> — Julia Roberts

1. ECOLOGICAL ASSEMBLY IS COMPLEX

Every budding naturalist knows that the order in which species arrive matters—"early birds get the worm". From a barren patch of earth transforms into a bustling forest, or a volcanic crater lake awakens with a chorus of life, every ecological community is a story written over time. But just how important is the order of arrival? Can we actually predict the winners and losers in this ecological Game of Thrones? This enigma, known as *ecological assembly*, lies at the very heart of ecological inquiry (Kraft & Ackerly, 2014; Mittelbach & McGill, 2019).

Figuring out the rules of ecological assembly matters a lot more than just academic bragging rights at conferences. It concerns real-world implications, from conserving biodiversity under changing climate (Dirzo et al., 2014), to managing the complex communities of bacteria in our own guts that can mean the difference between health and disease (Olm et al., 2022). Yet, for all its importance, our understanding remains fragmented, with more questions than answers.

The uncomfortable truth is, assembly can be fiendishly complex. Even when we don the theoretician's hat and strip away the complexities of nature, the problem remains formidable. The Lotka-Volterra model, a standard workhorse to understand community assembly (Tess Nahanni Grainger, Letten, et al., 2019; HilleRisLambers et al., 2012; Song et al., 2020), becomes a mathematical quagmire as the number of species grows, with multi-species dynamics capable of exhibiting virtually any dynamical behavior (Smale, 1976).

So, are we doomed to scratch our heads in perpetuity about ecological assembly? Not necessarily. Nature may operate on surprisingly simple principles (Friedman et al., 2017; Goldford et al., 2018). Some ecologists see assembly as a predictable progression, akin to the development of an organism, leading to a stable "climax" community (Clements, 1916; Odum, 1969). Others, however, emphasize the role of chance and individuality, such as the random colonization of islands (Theory of Island Biogeography; MacArthur & Wilson (2001)) or a neutral process where species are interchangeable (Neutral Theory of Biodiversity; Hubbell (2005)). Both perspectives, despite their differences, hint at the possibility of predictability under certain conditions. In contrast, there's a third camp that sees assembly as a maddeningly complex process, a tapestry woven from countless threads of environmental factors, species interactions, and historical contingencies. In their view, the sheer number of variables makes prediction a fool's errand (Lawton, 1999).

These seemingly contradictory viewpoints—super-organisms versus loose collections (Liautaud et al., 2019; Zelnik et al., 2024), or determinism versus chance (HilleRisLambers et al., 2012; Menéndez-Serra et al., 2023)—have long fueled debates in ecology. However, these debates are largely centered on the mechanisms of dynamical processes. What if, instead of getting bogged down in details, we take a step back and look at a bigger picture. Here's a different way to think about it: *Assembly is a process of reducing uncertainty*, of creating order within the bounds of ecological principles (Margalef, 1973). See, ecological assembly is a game of chance, sure, but it's a game with rules. Think of it like poker: the cards you're dealt are random, but the hand you play, the strategies you use, those are shaped by the rules of the game. In the ecological assembly, the "cards" are the species that show up, and the "rules" are the ecological interactions and environmental conditions that determine which ones thrive. Just as a skilled poker player can make predictable decisions despite the randomness of the deal, the ultimate community is more predictable than the vagaries of species arrival. This is not tautology, because if the community dynamics is completely stochastic, ecological assembly could possibly amplify the uncertainty in species arrivals.

Some might argue that the information perspective, with its roots in physics (Schrodinger, 1946), is an odd fit for ecology (Egler, 1986). I will show that this idea of viewing assembly as uncertainty reduction is not a figurative analogy, but instead, a powerful lens through which we can unify seemingly disparate ecological theories. The main mathematical tool we will use is called assembly graphs. The assembly graph is not a new idea at all (Hang-Kwang & Pimm, 1993; Law & Morton, 1993), but has seen a recent surge of interests spanning across a vast variety of theoretical tools (Almaraz et al., 2024;

Angulo et al., 2021; Coyte et al., 2021; Deng et al., 2024; Hofbauer & Schreiber, 2022; Lee et al., 2023; Leibold et al., 2019; Serván & Allesina, 2021; Song et al., 2021; Spaak & Schreiber, 2023).

In the remainder of this paper, I'll lay out a roadmap for how to use this assembly graph idea to get a handle on ecological assembly. First, we'll define assembly graphs and see their versatility with some simple examples. Then, we'll use assembly graphs to formalize the informational perspective. Next, we'll show how to break down these complex graphs into simpler pieces that are ecologically meaningful and experimentally measurable. From there, we'll look at how the topological patterns of the graph alone can already tell us whether species can robustly coexist via assembly. Then, we'll discuss how to deal with our incomplete knowledge with a probabilistic approach. After that, we'll see how different ecological models—the rules of species interactions—leave their mark on the topology of these graphs. Finally, I'll briefly discuss emerging approaches to infer assembly graph *empirically*, and point out some big theory puzzles still out there.

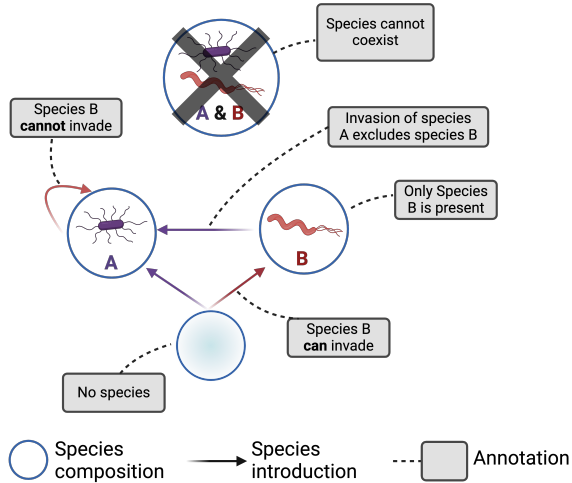## 2. Ecological Assembly as a Walk on Assembly Graph

A trail map does not just show where things are, but where they could go. That's the essence of an assembly graph in ecology. It documents the potential routes a community's composition can take as species come. Each point on this map represents a unique combination of species, and the paths connecting them show how new species can integrate into the community or how existing ones might disappear. The assembly graph allows us to trace how community composition can possibly develop along assembly processes.

Let's start with a simple example to get our feet wet. Picture a species pool with just two microbes, which we'll call A and B, and species A outcompetes species B (Figure 1a). Here's how we'd construct our assembly graph. First, we identify which species combinations are persistent, meaning all species within can survive. In total, there are four possible species combinations: no species ($\{\varnothing\}$, represented by the empty set symbol), species A only ($\{A\}$), species B only ($\{B\}$), and both species coexist ($\{A, B\}$). We represent these four combinations as nodes in our graph. In this specific case, A and B can't coexist as A competitively excludes B, so we remove the $\{A, B\}$ node.
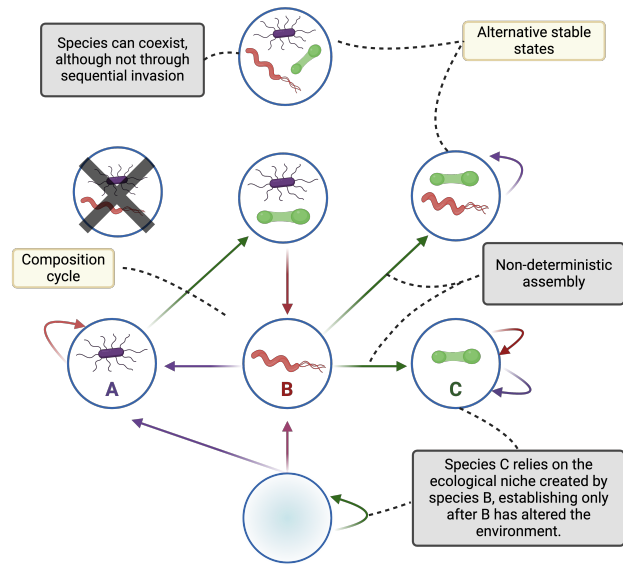
Next, we map out how species combinations change after an invasion. This creates the links in our graph, shifting the community from one composition (node) to another:

- $\{\varnothing\} \xrightarrow{A \text{ invades}} \{A\}$ (A can invade an empty community)
- $\{\varnothing\} \xrightarrow{A \text{ invades}} \{B\}$ (B can invade an empty community)
- $\{B\} \xrightarrow{A \text{ invades}} \{A\}$ (A can invade a community with only B and exclude it)
- $\{A\} \xrightarrow{B \text{ invades}} \{A\}$ (B cannot successfully invade)

This simple example gives us a clear picture of how assembly operates. But let's be honest, nature is rarely this tidy. So, let's throw a wrench in the works and introduce a third species C into the species pool. Suddenly, our simple graph witnesses a surge in complexity (Figure 1b). For instance, species C cannot establish itself in isolation, but it can if species B invades first and alters the environment (e.g., by changing the pH level) to make it hospitable for C. Moreover, species B might exhibit multi-stability or undergo inherent drift processes, meaning the invasion of C could lead to two outcomes: either

(a) A simple assembly graph with 2 species
[*Species A deterministic excludes Species B*]

Species cannot coexist

Species B **cannot** invade

A & B

Invasion of species A excludes species B

Only Species B is present

A

B

Species B **can** invade

No species

○ Species composition   → Species introduction   ---□ Annotation

(b) Complexity of ecological assembly

Species can coexist, although not through sequential invasion

Alternative stable states

Composition cycle

Non-deterministic assembly

A

B

C

Species C relies on the ecological niche created by species B, establishing only after B has altered the environment.

Figure 1 — **Illustration of Assembly Graphs.** Panel (a) shows a simple assembly with two species, labeled A and B. The nodes (blue) denote possible species compositions: $\{\varnothing\}$ (no species), $\{A\}$ (only species A present), $\{B\}$ (only species B present), and $\{A, B\}$ (both species coexist). Since species A are competitively superior to B, they cannot coexist, and thus we remove the node $\{A, B\}$ from the assembly graph (denoted by a cross sign). The links denote possible transitions between compositions through species invasions (purple line denoting species A invading and red denoting B invading). Panel (b) introduces a third species C into the same community. The resulting assembly graph exhibits a wider range of ecological phenomena, including non-deterministic assembly (multiple possible outcomes following one invasion), composition cycles (repeated transitions between compositions), and niche modification (early-arriving species alter the environment, thus changing the available niches for subsequent species).

species C alone or species B and C coexist. Additionally, we encounter two stable state—community compositions that, once reached, don't change. One of these states, where all three species coexist, cannot be reached through sequential invasions. These assembly scenarios highlight the flexibility of the assembly graph framework, accommodating multi-stability (Lopes et al., 2024), stochasticity (Zhou & Ning, 2017), environmental modification (Amor et al., 2020) — all of these have been observed in nature.

The assembly graph enables us to characterize community composition with arbitrary arrival orders. Consider the arrival order of B first, then A, and finally C. Using the assembly graph in Figure 1b, we trace the development path of community composition:

$$\{\varnothing\} \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\} \xrightarrow{C \text{ invades}} \{A, C\}$$

We can also consider multiple arrivals, such as allowing species B and C invade more than once:

$$\{\varnothing\} \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\} \xrightarrow{C \text{ invades}} \{A, C\} \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\}$$

The sole assumption we make is that invasions are rare, excluding simultaneous invasions of two or more species (Lockwood et al., 1997). This assumption offers greater flexibility compared to previous approaches that imposed stricter conditions. For instance, some models mandated that invaders pos-

sess low density while the invaded community remains at equilibrium (Serván & Allesina, 2021), or that ecological dynamics adhere to deterministic rules with fixed parameters irrespective of arrival orders (Spaak & Schreiber, 2023). The framework here transcends these limitations is because we allow multiple possible outcomes after an invasion (represented by multiple outgoing links from a node). This inherent flexibility empowers the assembly graph to encapsulate a broader spectrum of ecological scenarios.

3. ECOSYSTEM AS AN "ENGINE" OF UNCERTAINTY REDUCTION

Now, you might be thinking, "Isn't this assembly graph just another way of restating the problem?" But bear with me, because this change in perspective shifts our focus away from the details of ecological processes and towards a broader, more phenomenological view that's of the right complexity for formalizing the informational perspective of ecological assembly.

We can envision the ecosystem as an engine, processing the "raw material" of random arrival orders and producing a more structured, less uncertain community (Margalef, 1973; Song et al., 2021). By comparing the initial "messiness" of the arrival orders to the final "orderliness" of the community, we can quantify the amount of uncertainty the ecosystem has "absorbed" during assembly. The assembly graph is our tool for doing just that, without needing to know the specific ecological processes at play.

Let's make this concrete. We use the notation $\underline{\ldots}$ to denote the arrival orders, also known as *assembly history* (Fukami, 2004). For example, $\underline{ACB}$ means species A arrives first, then species C, and finally species B. With a species pool of two species, each arriving only once, we have two possible arrival orders: $\underline{AB}$ and $\underline{BA}$. For three species, we have six possibilities: $\underline{ABC}, \underline{ACB}, \underline{BAC}, \underline{BCA}, \underline{CAB}, \underline{CBA}$.
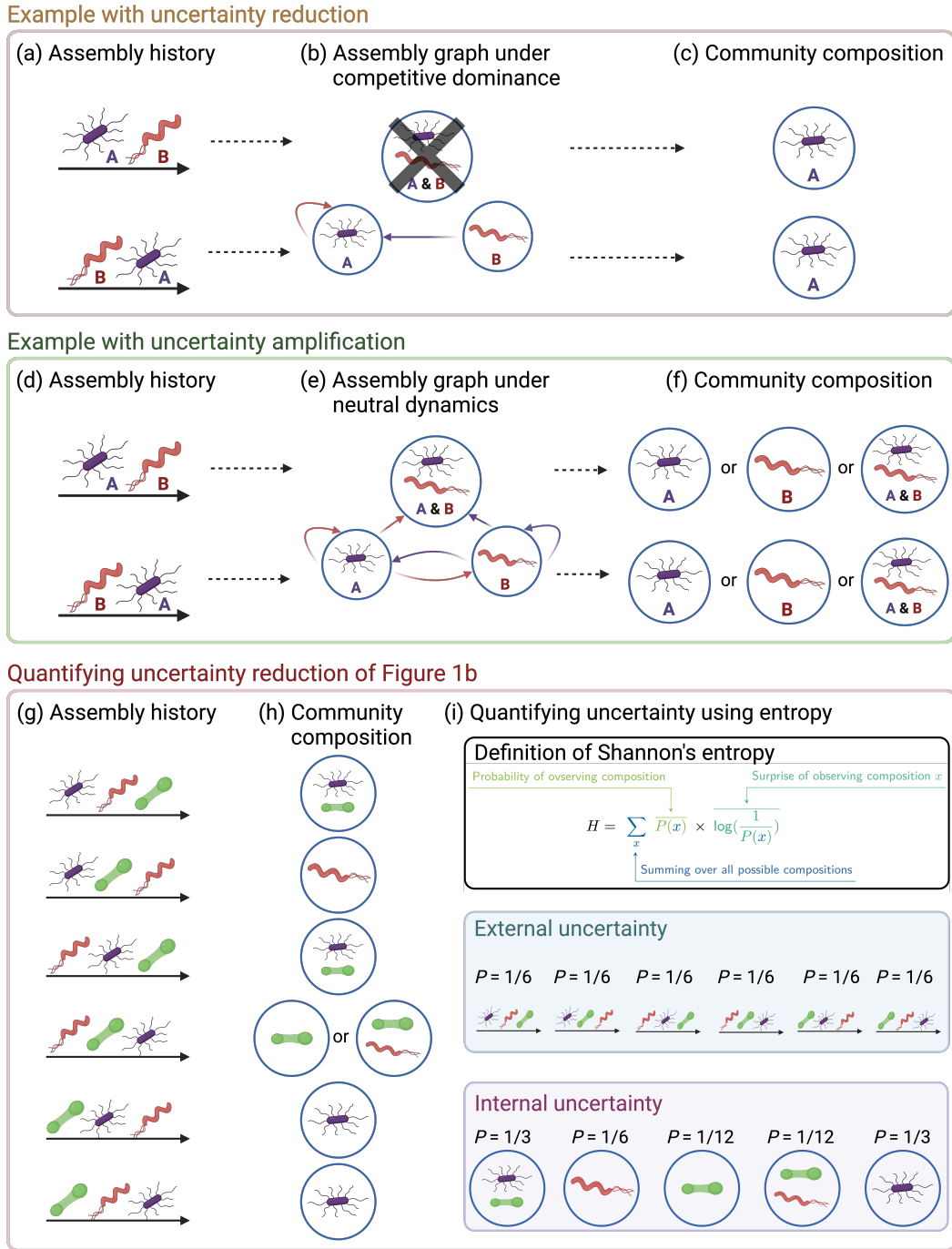
It's always helpful to consider the extremes. On one end, if every arrival order leads to the same final community, then uncertainty is completely eliminated. Figure 2a-c show an example where species A is competitive dominant over species B. In this case, both arrival orders $\underline{AB}$ and $\underline{BA}$ lead to the same outcome: a community consisting only of species A. On the other end of the spectrum, if every arrival order leads to a completely different community, or if all possible communities are equally likely, then the ecosystem does not reduce uncertainty or might even increase it. Figure 2d-f illustrates this with a neutral scenario, where the invasion of a species could lead to any outcome with equal probability. The community composition becomes even more unpredictable (three equal possibilities) than arrival orders (two equally probable possibilities).

Of course, in nature, things are rarely so clear-cut. To figure out where exactly a given ecosystem falls on this spectrum, we need a way to quantify uncertainty. That's where information theory comes in, specifically Shannon's entropy (H):

$$H = \sum_x P(x) \log\left(\frac{1}{P(x)}\right),$$

where each x represents a different possible community composition, and $P(x)$ is the probability of that composition happening. The $\log$ term measures the "surprise factor"—the less likely a composition, the more surprised you'd be to see it ("huh, didn't see that coming!"). Thus, we can think of entropy as a measure of surprise: how surprised would you be, on average, by the final composition?

Let's go back to our example with three species (Figure 2a). The external uncertainty H_{ext}, or the "messiness" of the species arrival orders, is:

Example with uncertainty reduction

(a) Assembly history (b) Assembly graph under competitive dominance (c) Community composition

Example with uncertainty amplification

(d) Assembly history (e) Assembly graph under neutral dynamics (f) Community composition

Quantifying uncertainty reduction of Figure 1b

(g) Assembly history (h) Community composition (i) Quantifying uncertainty using entropy

Definition of Shannon's entropy

Probability of ovserving composition   Surprise of observing composition x

$$H = \sum_x \overline{P(x)} \times \log\left(\frac{1}{P(x)}\right)$$

Summing over all possible compositions

External uncertainty

$P = 1/6$ $P = 1/6$ $P = 1/6$ $P = 1/6$ $P = 1/6$ $P = 1/6$

Internal uncertainty

$P = 1/3$ $P = 1/6$ $P = 1/12$ $P = 1/12$ $P = 1/3$

Figure 2 — **Quantifying Uncertainty Reduction in Ecological Assembly**. The top row (brown box) presents a case of complete uncertainty reduction under competitive dominance, where two possible species arrival orders (panel a) converge to a single final community composition (panel c) through an assembly graph (panel b) with species A competitively excluding species B. The middle row (green box) demonstrates uncertainty amplification under neutral dynamics, where two arrival orders (panel d) lead to three equiprobable community compositions (panel f) via an assembly graph (panel e) lacking competitive interactions. The bottom row (purple box) quantifies uncertainty reduction for a three-species assembly using Shannon's entropy (panel i). Panel (g) shows six equiprobable species arrival orders, while panel (h) depicts the assembly graph leading to five possible final community compositions with varying probabilities. Comparing external (initial) uncertainty to internal (final) uncertainty reveals a 20% reduction in uncertainty due to ecological processes.

$$H_{\text{ext}} = 6 \times \left(\tfrac{1}{6} \times \log(6) \right) = \log(6).$$

This makes sense: there are six equally likely arrival orders, so any particular one is fairly surprising.

Now, let's look at the internal uncertainty H_{int}—the uncertainty in the final community composition. As seen in Figure 2b, we have that

$$H_{\text{int}} = \underbrace{\tfrac{1}{3}\log(3)}_{\{A\}} + \underbrace{\tfrac{1}{6}\log(6)}_{\{B\}} + \underbrace{\tfrac{1}{12}\log(12)}_{\{C\}} + \underbrace{\tfrac{1}{3}\log(3)}_{\{A,C\}} + \underbrace{\tfrac{1}{12}\log(12)}_{\{B,C\}} = \log\left(3\sqrt{2}\right).$$

This is lower than the external uncertainty, which means the ecosystem has indeed reduced some uncertainty during assembly. The relative reduction in uncertainty is then:

$$H_{\text{reduction}} = \tfrac{H_{\text{int}} - H_{\text{ext}}}{H_{\text{ext}}} \approx 20\%.$$

In other words, the ecosystem has "absorb" about 20% of the external uncertainty.

We can even take this analysis down to the level of individual species. Each species within the community might have its own degree of uncertainty reduction. For instance, a species that doesn't interact much with others, occupying its own niche, would have its uncertainty completely reduced: as long as it arrives, regardless of when, it will establish. On the other hand, a species whose persistence depends heavily on when it arrives relative to other species wouldn't have its uncertainty reduced at all—it's unpredictable and at the mercy of chance. Thus, even within the same community, different species can experience different levels of predictability. In our old friend example (Figure 1b and Figure 2g-h), the relative reduction is 42% for species A, 36% for species B, and 49% for species C.

This information-theoretic perspective allows us to compare different theoretical models, as well as different empirical ecosystems, based on their capacity to reduce uncertainty. As long as we can derive the assembly graph, we can easily perform the analysis with varying assumptions. For example, we can also allow every species to invade more than once (Hewitt & Huxel, 2002), or follow some seasonal pattern (Zou et al., 2023).

4. BREAKING IT DOWN: BUILDING BLOCKS OF COMMUNITY ASSEMBLY

By now, you might be thinking, "Sure, this assembly graph sounds nifty, but isn't it just trading one headache for another?" And you'd be right to wonder. Indeed, as species numbers increase, we're not dealing with a simple linear progression, but facing a combinatorial explosion—each species either present or absent, the possible compositions multiplying rapidly. And that's before we even start mapping all the potential pathways connecting them. Previous studies have shown that the number of topologically different assembly graphs explodes super-exponentially as the number of species increases (Song et al., 2021).

The challenge, then, is to make sense of the labyrinth of complexity. Luckily, we're not the first to grapple with this issue: Interaction networks, where nodes represent species and links represent their interactions, are a cornerstone of community ecology and face similar issues (Coyte et al., 2015; Montoya et al., 2006). If we try to map out every pairwise interaction, even a modest number of species can quickly lead to an overwhelming number of links. In most natural systems, documenting the full interaction network is a Herculean task. But ecologists aren't after the full map for its own sake. We

want to know what the network structure *reveals* about the community's properties, such as its stability in the face of disturbances or its response to environmental change (Kaiser-Bunbury et al., 2017; Tylianakis & Morris, 2017).

Rather than drowning in the full interaction network, ecologists have long focused on smaller, recurring patterns within networks, known as motifs or modules (Stone et al., 2019). For example, food webs often exhibit tri-trophic chains (a linear feeding relationship with three trophic levels) or apparent competition (where two species indirectly harm each other by supporting a common enemy) (Bonsall & Hassell, 1997; Holt, 1977; Morris et al., 2004). These motifs are the ecological equivalent of catchy tunes—they're easy to spot (less sensitive to sampling bias), and they tell us a lot about how the system functions (e.g., informative of stability) (Simmons et al., 2019; Song et al., 2023). This 'divide and conquer' approach has proven to be incredibly fruitful, not just in ecology, but across biology, from gene regulation (Alon, 2007) to brain function (Sporns & Kötter, 2004).

Switching back to ecological assembly, ecologists have already, drawing on natural histories, identified some assembly patterns that appear repeatedly across diverse communities (Fukami, 2015):

- **Alternative Stable States** (Gilpin & CASE, 1976; Schooler et al., 2011; Schröder et al., 2005): community can settle into multiple stable compositions. Graphically, it means that the assembly graph has more than one "sink"—nodes that have incoming links but no outgoing link (Figure 3a). It's common in nature (Scheffer et al., 2001): lakes can exist in either a clear state with abundant submerged vegetation or a turbid state with phytoplankton dominance (Carpenter & Cottingham, 1997); coral reefs can exist in either a healthy state dominated by corals or a degraded state dominated by algae (Hughes, 1994). Mechanistically, this can arise from early-arriving species either hogging the best resources (niche preemption) or reshaping the environment (niche modification) (Figure 3a).

- **Alternative Transient Paths** (Fukami & Nakajima, 2011; 2013; Sarneel et al., 2019): Multiple routes exist for a community to reach a stable state. Graphically, it means that the assembly graph has more than one directed path exist from empty to a sink (Figure 3b). For example, in a newly exposed patch of soil, a nitrogen-fixing bacterium may arrive first, paving the way for other microbes, or a fungus might arrive first, improving soil structure for different nitrogen-fixing bacteria. In both scenarios, a diverse and stable microbial community eventually forms, but their order of arrival may vary.

- **Compositional Cycles** (Fox, 2008; Schreiber & Rittenhouse, 2004): assembly process can go in circles, with the community cycling through a series of changes before returning to a previous composition. Graphically, it means that the assembly graph has directed cycles (Figure 3c). This can also occur in nature, especially with the rock-paper-scissor dynamics. For example, colicin-producing bacteria kill sensitive ones, resistant bacteria outcompete producers, and sensitive bacteria outgrow resistant ones due to lower metabolic costs (Kerr et al., 2002; Kirkup & Riley, 2004).

We call these building blocks *assembly motifs*. By focusing on these assembly motifs, we start untangling what feature of assembly contribute to uncertainty reduction. In a rough analogy, it's like predicting where skiers end up: if all trails lead to the same lodge (i.e., no alternative stable states), it's easy. The presence of multiple lodges makes prediction more difficult (i.e., with alternative stable states), but if some lodges have many trails leading to them while others have few (alternative transient paths),
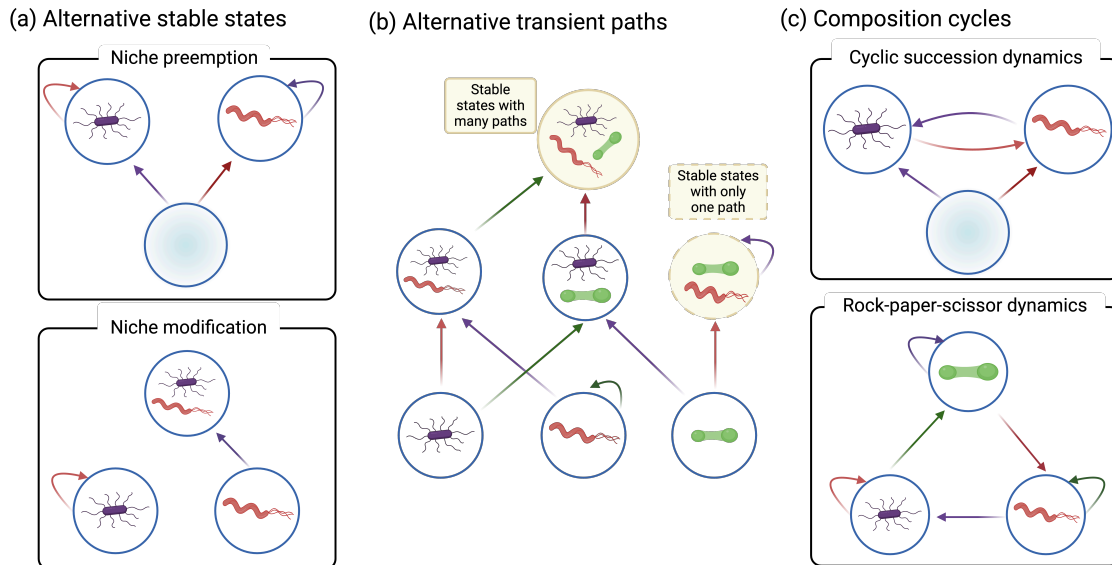
Figure 3 — **Assembly motifs as building blocks of assembly graph**. This figure illustrates three common assembly motifs found in ecological assembly. Panel (a) shows alternative stable states, where multiple stable community compositions (nodes with no outgoing links) can arise from the same initial conditions and species pool, often due to niche preemption (early arrivers monopolize resources) or niche modification (early arrivers alter the environment). Panel (b) shows alternative transient paths, where multiple arrival orders can lead to the same stable state. As a consequence, some stable states are more probable than others. Panel (c) shows composition cycles, where communities can exhibit cyclical changes in composition, such as through cyclic succession (e.g., seasonal changes) or rock-paper-scissors dynamics (e.g., species interactions where species A outcompetes B, B outcompetes C, and C outcompetes A).

prediction becomes easier. Looping tails (like backcountry skiing) add unpredictability (compositional cycles). These patterns all affect uncertainty reduction of the assembly process.

However, are these assembly motifs enough to explain the uncertainty reduction? Almost. The missing piece is whether cycles have "escape routes"—once a community enters a compositional cycle, can it exit? This kind of escape has been observed in nature (Drake, 1991). The presence or absence of escape routes can significantly impact the overall predictability of the assembly process. Past work, assuming single outcomes post-invasion, shows that these four motifs are enough to explain uncertainty reduction quite well (Song et al., 2021). Importantly, we need all four of them. Historically, most attention has been paid to the number of alternative stable states (Abreu et al., 2020; Amor et al., 2020; Schröder et al., 2005). But, especially in small communities, the other three motifs can play an even bigger role in reducing uncertainty than alternative stable states (Song et al., 2021).

5. Robust Coexistence via Assembly Graph

So far, we have not specified the meanings of the links in the assembly graph (what does transition means, both in theory and through empirical observation). A natural approach is invasion analysis—a method with deep roots in ecological research (Tess Nahanni Grainger, Levine, et al., 2019; MacArthur & Levins, 1967). In essence, we begin with a resident community at equilibrium and then introduce a new species at low density. For instance, if we're curious about whether species A and B can coexist, we first establish a community solely composed of species A and observe if species B can successfully

invade. We then repeat the process, starting with a community of only species B and seeing if species A can invade.

But a pivotal question arises: Does the ability to invade guarantee coexistence? To answer this, we need to clarify what we mean by "coexistence". Unfortunately, many traditional metrics, such as local or global stability, are overly restrictive. They require the system to remain at equilibrium indefinitely, a condition rarely found in nature. For ecologists and conservationists, the core of coexistence is that over a long period of time, species abundance can have ebbs and flows, but won't dwindle to zero or explode to infinity. In this sense, a concept called *permanence* is far more relevant. Permanence means that, regardless of the initial conditions, species populations are bounded above zero and some finite maximum. Permanence embraces the fluctuations that characterize natural communities (Pennekamp et al., 2019; Rogers et al., 2022), while treating traditional metrics like global stability as merely a special case. Therefore, permanence is a more natural and meaningful way to define coexistence.

However, permanence is less used because it is typically difficult to verify. Excitingly, there's a direct and rigorous link between the assembly graph and the permanence of a stable state. Here we briefly review this exciting recent advance in the mathematical theory of permanence (Almaraz et al., 2024; Hofbauer & Schreiber, 2022; Spaak & Schreiber, 2023). The sole prerequisite is that the invasion graph must be acyclic, meaning it lacks cyclical patterns of community composition. When the acyclicity holds, a community is permanent *if and only if* each of its coexisting subcommunities can be invaded by at least one species. This is not a mere rule of thumb; it's a rigorously proven theorem.

The beauty of this criterion lies in its visual clarity and ease of application. Let's illustrate with the assembly graph in Figure 4. First, we confirm it's acyclic. Then, we identify the two stable states (nodes with no outgoing links): one with species A, B, and C, and another with species C and D. Focusing on $\{A, B, C\}$, we check each of the subcommunities: $\{\varnothing\}, \{A\}, \{B\}.\{C\}, \{A, B\}, \{A, C\}$. Note that we omit $\{B, C\}$ because B and C cannot coexist. This is inconsequential, as the criterion pertains only to coexisting subcommunities. We then check if each of these subcommunities can be invaded (has an outgoing link), which is indeed the case. Thus, the $\{A, B, C\}$ is permanent.

In contrast, for the other stable state $\{C, D\}$, while the subcommunities $\{C\}$ and $\{D\}$ can be invaded, the empty community $\{\varnothing\}$ cannot. This could happen, for instance, due to an Allee effect (Kaul et al., 2016). A case in point is the *Streptococcus pneumoniae* bacteria, which relies on quorum sensing to coordinate its virulence. At low densities, the bacteria cannot effectively communicate and launch a coordinated attack, making it difficult to establish (Moreno-Gámez et al., 2017; Weiser et al., 2018).

This graphical criterion almost seems too good to be true. It's easy to verify (we just need to look at a graph, not complex equations), mathematically rigorous (unlike most heuristic criteria of coexistence), and directly applicable to natural communities (as permanence allows for the fluctuations inherent in these systems). And if that weren't enough, it also ties in with Modern Coexistence Theory, a leading framework for studying species coexistence (Barabás et al., 2018; Chesson, 2000; Song et al., 2019). Modern Coexistence Theory has gained widespread acceptance among empirical ecologists studying community assembly (HilleRisLambers et al., 2012; Kraft & Ackerly, 2014). However, the validity of assembly based on the invasion criterion has been a subject of intense debate, raising concerns about the framework's applicability to empirical data (Arnoldi et al., 2022; Barabás et al., 2018; Pande et al., 2020). The new theory (Almaraz et al., 2024; Hofbauer & Schreiber, 2022; Spaak & Schreiber, 2023)
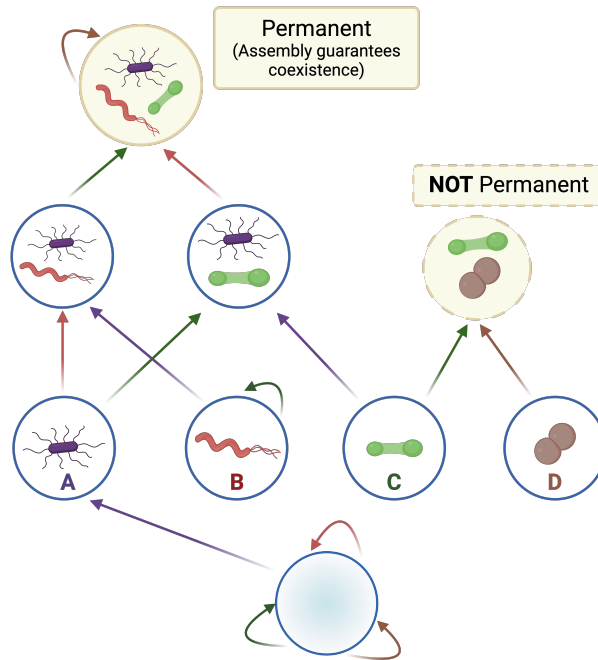
Figure 4 — **Graphical Criterion for Robust Coexistence**. This figure illustrates a graphical criterion for determining the robust coexistence (permanence) of species within a community, using an assembly graph. The criterion states that a community is permanent if and only if each of its coexisting subcommunities can be invaded by at least one species from the regional pool. In this example, the stable state $\{A, B, C\}$ (a node with no outgoing links) is permanent because all its coexisting subcommunities (those without species D) can be invaded. However, the other stable state $\{C, D\}$ is not permanent because the empty community cannot be invaded, potentially due to an Allee effect where neither species C nor species D can establish at low densities.

effectively resolves this long-standing debate and presents a promising avenue, providing a robust foundation for testing this approach in real-world ecosystems.

6. EMBRACING IGNORANCE: A PROBABILISTIC VIEW OF ASSEMBLY

So far, all the links in our assembly graph have been binary—either a transition between states is possible or it isn't. But nature rarely deals in such absolutes. The ecological dynamics underlying assembly might be inherently random (Obadia et al., 2017; Vega & Gore, 2017). The environment, too, is a maelstrom of change, with shifts in temperature or resource availability (Debray et al., 2022; Jones et al., 2022). And even if, for the sake of argument, we assume a deterministic assembly process in a static environment, our knowledge of the system is always incomplete, rendering assembly probabilistic in practice.
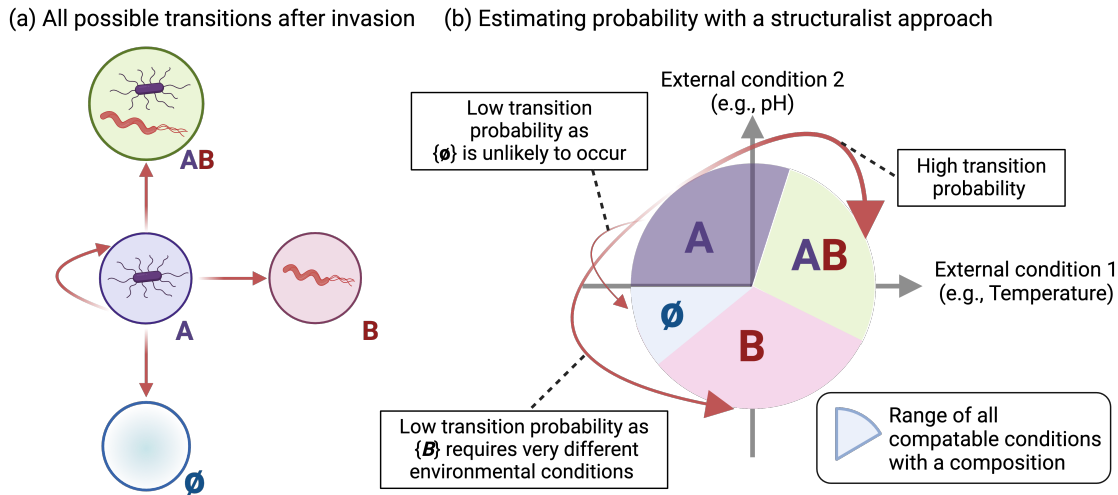
How do we grapple with this uncertainty? We can adopt a two-pronged approach. The first approach is a matter of statistical rigor, to acknowledge that our models and data are imperfect and to quantify the errors inherent in our analyses (Terry & Armitage, 2024). This kind of statistical rigor is increasingly becoming the norm in the field (Bowler et al., 2022; Hess et al., 2022; Majer et al., 2024).

But there's another, complementary approach, one that seeks to estimate uncertainty based on the very structure of the ecological community itself (Alberch, 1989; Gould, 2002). The idea is that some communities are inherently more likely to occur than others, simply because their structures are com-

patible with a wider range of environmental conditions (Saavedra et al., 2017; Song, 2020). How do we use this approach to estimate the likelihood of transitions between communities? There are two forces at play (Long et al., 2024): how likely the transitioned composition can exist, and how similarly the two compositions need the environment. For the first force, it is easy to see that if the transitioned composition is compatible with a large range of environments, the transition is more likely. As for the second force, if we observe a particular community in nature, we can infer that the environmental conditions must be suitable for that community to exist. Now, if another community requires vastly different conditions, it's less likely that the system will transition from one to the other. Conversely, if two communities thrive under similar conditions, the transition between them is more probable. Formally, for the transition from composition X to composition Y, the probability is simply proportional to (Long et al., 2024):

$$P(\boldsymbol{X} \to \boldsymbol{Y}) \propto \overset{\substack{\text{Probability of} \\ \boldsymbol{Y} \text{ coexistent}}}{\Omega_Y} \Big/ \underset{\substack{\text{Dissimilarity between} \\ \text{compatible environments}}}{D_{X,Y}}$$

To illustrate, consider a simple community with only species A, which is then invaded by species B. There are several possible outcomes: the community could become empty $\{\varnothing\}$ (e.g., due to the enrichment paradox), B could fail to invade (leaving the community as $\{A\}$), A could be excluded (resulting in community $\{B\}$), or both species could coexist (community $\{A, B\}$). The transition to each of these

(a) All possible transitions after invasion   (b) Estimating probability with a structuralist approach

Figure 5 — **Estimating Transition Probabilities using a Structuralist Approach**. This figure illustrates how to incorporate our incomplete knowledge about ecosystems into assembly graphs by assigning probabilities to transitions (links) between species compositions (nodes). In panel (a), all possible transitions after the invasion of species B (red) into a community initially composed only of species A (purple) are shown. Panel (b) shows how the probability of each transition can be estimated using a structuralist approach. In this approach, the probability of a transition from composition X to composition Y is determined by two factors: the probability of the resulting composition existing (which is represented by the size of the area corresponding to that composition Y in the diagram, denoted by Ω_Y), and the dissimilarity between the environmental conditions compatible with the initial and final compositions (which is represented by the distance between the two compositions in the diagram, denoted by $D_{X,Y}$). Transitions are more likely if the resulting composition is probable (large Ω_Y) and the environmental conditions required by the two compositions are similar (small $D_{X,Y}$). In this example, composition with both species are most likely.

outcomes has a different probability. For example, the transition from $\{A\}$ to the empty community $\{\varnothing\}$ is possible but unlikely, because while the environmental conditions that support community $\{A\}$ are similar to those that result in an empty community, the empty community itself is unlikely to occur (i.e., $\Omega_{\{\varnothing\}}$ is small). The transition from $\{A\}$ to $\{B\}$ is also unlikely, because while community $\{B\}$ is itself likely, the environmental conditions that support it are quite different from those that support $\{A\}$ (i.e., large $D_{\{A\},\{B\}}$). The transition from $\{A\}$ to $\{A, B\}$ has the highest probability, because community $\{A, B\}$ is both likely in itself and the environmental conditions that support it are similar to those that support $\{A\}$ (i.e., large $\Omega_{\{A,B\}}$ and small $D_{\{A\},\{A,B\}}$).

In essence, this approach allows us to quantify our ignorance. We acknowledge that we don't have perfect knowledge of the system, but we use the information we do have—the structure of the community itself—to make informed predictions about its future. It's a way of embracing uncertainty, not as a roadblock, but as an integral part of the ecological puzzle. This approach has already shown promise in understanding the assembly of complex microbial communities (Deng et al., 2024; Long et al., 2024; Ogbunugafor & Yitbarek, 2024).

7. Linking Structure of Ecological Models and Topology of Assembly Graphs

So far, we have studied the assembly graph in its most general form and not restricted ourselves to any particular ecological dynamical model. But, like any good tool, it's even more useful when you have the right attachment for the job. In ecology, that attachment is the specific model—the rules it lays out for how species interact. The specific structure of an ecological model puts some serious limits on what can actually happen in ecological assembly. The cool thing is, these limits translate directly into the topology of assembly graphs we can get. It's like the model's DNA is written into the graph's shape.

To illustrate, let's take a classic example of two species competing for resources with MacArthur-type dynamics, a standard mechanistic model in ecology (Sakarchi & Germain, 2024; Tilman, 1982). Briefly, the model assumes the *fixed* ability of a species to consume a resource. Turns out, there are only three ways this can play out: one species always wins (no matter who arrives first; Figure 6a), both species live together (again, arrival order doesn't matter; Figure 6b), or whoever gets there first takes all (Figure 6c). That's it. These three outcomes represent the only possible topologies of the assembly graph for this model, out of all possible parameter values.

Now, you might be thinking, "Hold on, Mother Nature can be way more complicated than that!" And you'd be absolutely right. For instance, consider two microbiome species, A and B, competing for resources in a rough environment (Figure 6d). If the fast-growing, aggressive species A establishes first, it can dominate the available resources, hindering the subsequent establishment of the slower-growing, stress-tolerant species B. However, if species B arrives first, it can establish a foothold, allowing for coexistence with species A upon its later arrival. This necessitates expanding our model class. We can incorporate trait-mediated priority effects, where the ability to consume resources evolves with the order of species arrival (Rudolf, 2019; Zou et al., 2024). This expanded model class captures a wider range of ecological interactions, and generates three other possible topology of assembly graphs (Figure 6d-f).

Two species are easy to wrap our heads around, but what happens with more species? Ecologists have a running joke about understanding one, two, or infinite species, but nothing in between. Luckily, recent work has made real progress in understanding three-species competition systems (Lee et al.,
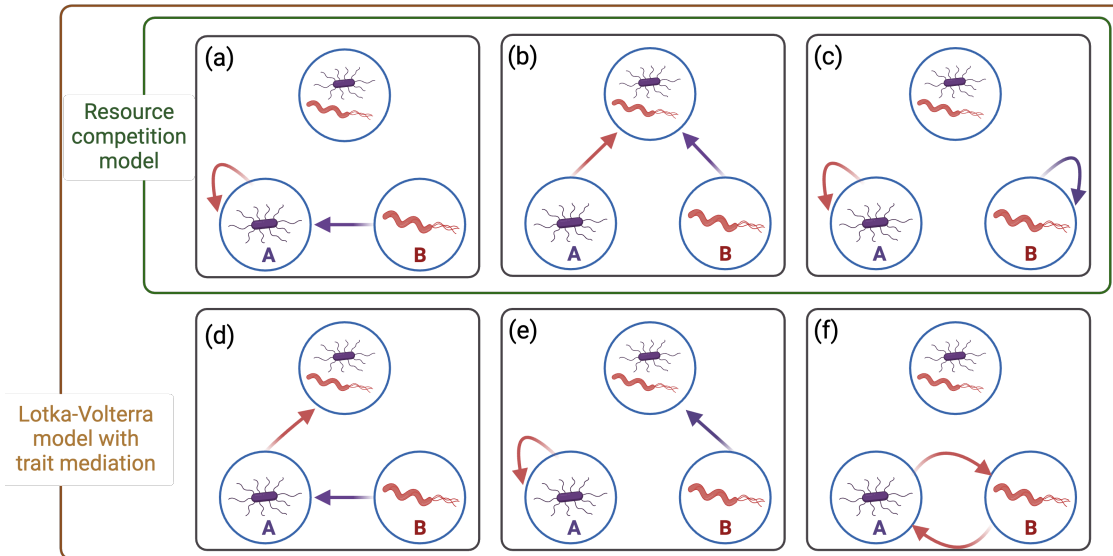
Figure 6 — **The class of ecological models constrains the topology of assembly graphs**. To illustrate, we consider all possible ecological assembly between two species, A and B. The MacArthur resource competition model (green box) assumes species' resource use is fixed regardless of arrival order. This class of model leads to three, and only three, assembly outcomes: deterministic exclusion (e.g., species *A* excludes species *B*; panel a), deterministic coexistence (*A* and *B* coexist stably; panel b), or priority effects (only the early arriving species persists; panel c). In contrast, the Lotka-Volterra model with trait-mediated interactions, where interactions change depending on arrival order, allow for three additional possibilities (panels d-f).

2023; Ranjan et al., 2024). They've found we can sort assembly graphs into different levels, depending on how complex the ecological model is: heuristic assembly rules (outcome of triplets depends only on the outcome of pairwise competitions), resource competition model, Lotka-Volterra dynamics with fixed interactions (species interactions are fixed regardless of arrival orders), and Lotka-Volterra dynamics with trait-mediated Interactions (species interactions are dependent on arrival orders). This categorization resembles a ladder, with each rung representing a different level of complexity in the ecological model.

How about for even more species? A brute-force classification might be beyond our reach. One way to tackle this is to look at properties other than the exact shape of the assembly graph. Just as mathematicians classify objects by the number of "holes" they have, ecologists have developed a similar approach for ecological assembly (Angulo et al., 2021; Letten, 2021). This has already led to some exciting progress in classifying how communities assemble (Flores-Arguedas et al., 2023).

Another approach is to look at the *typical* behavior of species-rich systems using well-established models with random interactions. This approach has a rich history in ecology (Bunin, 2017; May, 1972) and has proven valuable in microbiome research, which often deals with species-rich communities (Hu et al., 2022; Moran & Tikhonov, 2022). Some recent work has revealed a trade-off between reducing uncertainty (information perspective) and barriers to assembly (the assembly graph being disjoint, a topological pattern) (Coyte et al., 2021). Abnother line of recent work looks at when bottom-up assembly (building from individual species) and top-down assembly (starting with the full species pool) lead to the same final composition (Serván et al., 2018; Serván & Allesina, 2021).

In sum, there exists a direct correspondence between the *structure of ecological models* and the possible *topologies of assembly graphs*. The beauty of this connection between models and graphs is that we can use the topology of the assembly graph—which is directly observable without needing parameter estimation or fitting—to tell us if the very structure of model is likely to be wrong.

8. THE ASSEMBLY LINE STALLS: DERIVING EMPIRICAL ASSEMBLY GRAPH

The experimental derivation of assembly graphs remains scarce, with notable exceptions being the works of Drake (1991) and Warren et al. (2003). Why the scarcity? First, ecologists might not yet fully appreciate the potential of this emerging tool, often favoring established 'the tried and true' methods over the new kid on the block. Second, and more importantly, doing the actual experiments is *hard*. It's easy for a theorist like me to dream up an experiment on a napkin, but actually carrying it out in the field or the lab has to wrestle with the real world, which is never easy. Therefore, for systems exceeding the simplicity of 2- or 3-species cases amenable to brute-force approaches, the development of innovative experimental designs becomes imperative (Zou & Rudolf, 2023). While I clearly lack expertise in experimental ecology, I'd like to highlight two promising avenues that could address this empirical bottleneck.

One direction leverages the power of computational tools. The good news is that most assembly graphs are likely to be sparse (much like how most people have a limited number of close friends within a vast social network). Coexistence is, in general, rare (Angulo et al., 2021; Chang et al., 2023): the majority of species combinations are simply incompatible. This sparsity presents a significant advantage, as it allows computational algorithms to infer the structure of the assembly graph, even with incomplete experimental data. This direction is currently witnessing a surge in the development of mechanism-agnostic approaches, meaning they are likely to be generally applicable across ecosystems. Notable examples include deep-learning methods (Baranwal et al., 2022; Michel-Mata et al., 2022; Wu et al., 2024), Bayesian statistics (Lemos-Costa et al., 2023; Maynard et al., 2020; Skwara et al., 2023), and compressive sensing (Arya et al., 2023; Kempes, 2024).

Another exciting direction involves a shift in perspective, from focusing on individual species to their functional roles within the community. This represents a significant paradigm shift in community ecology in the past two decades, emphasizing traits and functional attributes over species identities (Fukami et al., 2005; McGill et al., 2006). In the context of microbiome research, it has become increasingly evident that predicting the functional capabilities of a community is often more tractable than predicting its precise species composition (Goldford et al., 2018; Louca et al., 2018; Tian et al., 2020). And there's even evidence suggesting that the effects of a species on community function might simply be additive (Diaz-Colunga et al., 2023; 2024). This observation opens up the intriguing possibility of "coarse-graining" assembly graphs, simplifying their structure by grouping species based on their functional roles (Frioux et al., 2023; Moran & Tikhonov, 2022; 2024). Such an approach could significantly reduce the size of assembly graphs, thereby facilitating their inference from empirical data.

9. OPEN THEORY QUESTIONS

While the theory of ecological assembly has witnessed many exciting progresses in recent years, it's far from a finished book. Many chapters remain unwritten, and some of the most exciting stories may lie in the unexplored corners. Here, I'll highlight two promising research directions that are extremely important but less traveled.

The first direction concerns multiple invasions occurring within a short time span. The assembly graph framework assumes a separation of timescales, where invasions happen sequentially and the community dynamics settle into equilibrium before the next invasion. It is as if asking species politely waiting their turn to join the community. However, natural communities might not be built in this way. Take, for instance, the classic rock-paper-scissors dynamics of three competing species, where all can coexist, but no pair can. This means you can't build this 3-species community one invasion at a time. A more detailed theoretical study shows that some species can only invade when others invade simultaneously (Lockwood et al., 1997). The authors dubbed this the "1066-effect", drawing a parallel to the Norman conquest of England, where William of Normandy's victory was aided by am invasion attempt by Harald Hardrada of Norway in the same year. This phenomenon isn't just theoretical musing; Empirical work has also shown that coexistence can be an emergent property (Chang et al., 2023), potentially not achievable through sequential invasions. Yet, our theoretical grasp of these simultaneous invasions is still in its infancy. One potential approach is to consider higher-order representations of the assembly graph (Arruda et al., 2024; Benson et al., 2016), where joint invasions are represented as hyper-dimensional links.

The second direction concerns the flip side of assembly: disassembly. While assembly focuses on the arrival of new species into a community, disassembly processes involve the loss of species due to factors like habitat fragmentation (Chase et al., 2020; Song et al., 2022) and climate change (Baldrian et al., 2023; Klink et al., 2024). Importantly, disassembly isn't simply assembly in reverse; it operates under its own set of ecological principles and requires the development of new theoretical frameworks (He & Hubbell, 2011; Storch et al., 2012). It's like a game of Jenga—extracting blocks (species) from an existing tower involves a different strategy than building it up. Recent research has begun bridging this gap, extending assembly concepts to the realm of disassembly. Drawing inspiration from the ecological mechanisms influencing community assembly (Fukami, 2015), studies have started unraveling the corresponding mechanisms that govern disassembly (Agostina Torres, Kuebbing, et al., 2024; Agostina Torres, Morán-López, et al., 2024). For another example, the concept of "assembly holes," used to classify assembly scenarios, has also found its counterpart in "disassembly holes", offering a parallel approach to classify disassembly scenarios (Angulo et al., 2021). Despite these advancements, the study of disassembly remains a nascent field compared to the wealth of research on assembly, highlighting the vast potential for future exploration.

10. SUMMARY

This paper offers an opinionated review of ecological assembly theory, using the assembly graph as its Rosetta Stone. The assembly graph is less of a traditional theory, but more like a language of assembly. Imagine wandering the Gothic Quarter of Barcelona without knowing a word of Spanish—it is possible but much less fun (Roughgarden, 1998). Using this new "language", I survey some recent exciting advances across informational, dynamical, and probabilistic approaches.

I center the informational perspective—assembly as uncertainty reduction—as the overarching foundation. This idea, harking back to Erwin Schrödinger's concept of life feeding on "negative entropy" (Schrodinger, 1946), has already proven valuable in guiding the development of biophysics (Avery, 2021; Jeffery et al., 2019). The information perspective is both conceptually intuitive and computationally feasible, providing a mechanism-agnostic umbrella to other approaches.

With the information perspective as a foundation, we can construct dynamical and probabilistic theories, and connect past theories to this new framework. I've focused on broad ideas and frameworks that are widely applicable. In particular, these ideas can be applied to most of the emerging dynamical models in microbiome ecology—including Lotka–Volterra model, consumer–resource model, trait-base model, or individual-based model, and Genome-scale metabolic models (Berg et al., 2022).

The assembly graph is a tool, not a panacea. It raises many questions (hopefully less than the questions it answers). Its applicability to diverse ecological systems remains to be fully explored. On the empirical front, advances in microbiome research have been a game-changer, providing an ideal testing ground for ecological theory and offering new insights into this long-standing problem (Gore & You, 2022; Picot et al., 2023). Of course, microbiomes differ in many ways from communities of animals and plants, so whether these principles hold true in those ecosystems remains an open question.

In a field often fragmented by specialized jargon and competing schools of thought, this paper is a call for unity. Beneath the surface complexity, there is hope for some fundamental principles that govern the assembly of ecological communities. This paper does not intend (nor possible) to provide an exclusive encyclopedia of ecological assembly theory. But rather, in the spirit of the Chinese proverb, 抛砖引玉 (tossing out a brick to attract jade), consider this an invitation to join this complex but absolutely fascinating world of ecological assembly.

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