



## PERSPECTIVE

# Assembly Graph as the Rosetta Stone of Ecological Assembly

Chuliang Song 

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

**Correspondence:** Chuliang Song ([clsong.ecology@gmail.com](mailto:clsong.ecology@gmail.com))**Received:** 1 August 2024 | **Revised:** 2 December 2024 | **Accepted:** 18 December 2024**Keywords:** assembly graph | ecological assembly | priority effect | species invasion**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 symbolise 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 catalyse 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

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 being healthy or diseased (Olm et al. 2022; Wu et al. 2024). Yet, for all its importance, our understanding remains fragmented, with more questions than answers.

## 1 | Ecological Assembly Is Complex

Every budding naturalist knows that the order in which species arrive matters—‘The early bird gets 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 and Ackerly 2014; Mittelbach and McGill 2019).

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 (HilleRisLambers et al. 2012; Grainger et al. 2019; Song et al. 2020), becomes a mathematical quagmire as the number of species grows, with multi-species dynamics capable of exhibiting virtually any dynamical behaviour (Smale 1976).

Figuring out the rules of ecological assembly matters a lot more than just academic bragging rights at conferences. It concerns

So, are we doomed to scratch our heads in perpetuity about ecological assembly? Not necessarily. Nature may

operate on surprisingly simple principles (Friedman, Higgins, and Gore 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, emphasise the role of chance and individuality, such as the random colonisation of islands (Theory of Island Biogeography; MacArthur and 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 is 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 fuelled debates in ecology. However, these debates are largely centred 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 is 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 is a game with rules. Think of it like poker: the cards you are 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 predictive decisions despite the randomness of the deal, the ultimate community is more predictable than the vagaries of species arrival. This is not a 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 representation we will use is called assembly graphs. The assembly graph is not a new idea at all (Law and Morton 1993; Hang-Kwang and Pimm 1993), but has seen a recent surge of interests spanning across a vast variety of theoretical tools (Song, Fukami, and Saavedra 2021; Serván and Allesina 2021; Coyte et al. 2021; Hofbauer and Schreiber 2022; Spaak and Schreiber 2023; Leibold et al. 2019; Angulo et al. 2021; Lee, Bloxham, and Gore 2023; Almaraz et al. 2024; Deng et al. 2024; Godoy et al. 2024).

The rise of theory in assembly graphs is perfectly timed with the rapid progress in experimental microbiology. Microbes are ideal for testing and refining ecological theory (Prosser et al. 2007; Gore and You 2022; Picot et al. 2023): They reproduce quickly, we can control their environments precisely, and we can track them with incredible detail—all of which is rarely possible with

macro-organisms (Kehe et al. 2019; Dal Co et al. 2020). For example, recent microbial experiments have tested a range of core ecological theories (Dai et al. 2012; Batstone et al. 2020; Gowda et al. 2022; Chang et al. 2023). This synergy of powerful theory and tractable experiments makes now an opportune moment to study community assembly.

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

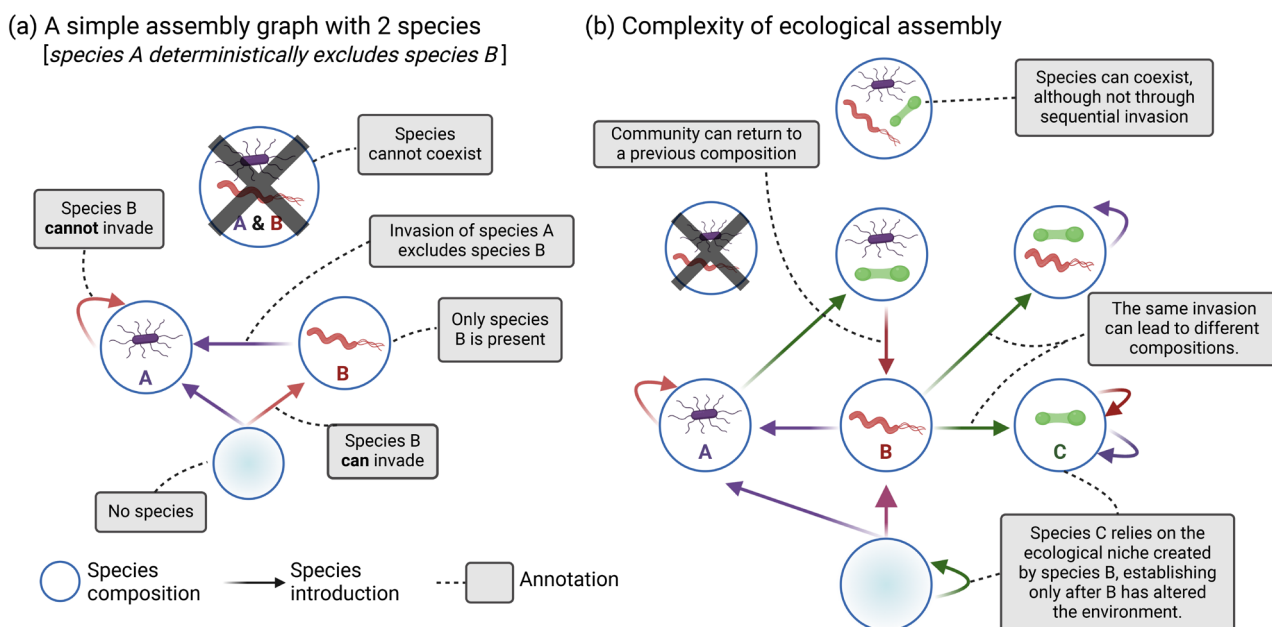
## 2 | Ecological Assembly as a Walk on Assembly Graph

A trail map does not just show where things are, but where they could go. That is 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 go extinct. The assembly graph allows us to trace how community composition can possibly develop along assembly processes.

Let us start with a simple example to get our feet wet. Picture a species pool with just two microbes, which we will call *A* and *B*, and species *A* outcompetes species *B* (Figure 1a). Here is how we would 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 ( $\emptyset$ , 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* cannot 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:

- $\emptyset \xrightarrow{A \text{ invades}} \{A\}$  (*A* can invade an empty community).
- $\emptyset \xrightarrow{B \text{ invades}} \{B\}$  (*B* can invade an empty community).
- $\{B\} \xrightarrow{A \text{ invades}} \{A\}$  (*A* can invade a community with only *B* and exclude it).



**FIGURE 1** | Illustration of assembly graphs. Panel (a) shows a simple assembly with two species, labelled A and B. The nodes (blue circle) denote possible species compositions:  $\emptyset$  (no species), {A} (only species A present), {B} (only species B present), and {A, B} (both species coexist). Assuming 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), compositional cycles (repeated transitions between compositions), and niche modification (early-arriving species alter the environment, thus changing the available niches for subsequent species).

- $\{A\} \xrightarrow{B \text{ invades}} \{A\}$  (B cannot successfully invade).

This simple example gives us a clear picture of how assembly operates. But let us be honest, nature is rarely this tidy. So, let us 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 species C alone or species B and C coexist. Additionally, we encounter two stable states—community compositions that, once reached, do not 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, Amor, and Gore 2024), stochasticity (Zhou and Ning 2017), environmental modification (Amor, Ratzke, and Gore 2020)—all of these have been observed in nature.

The assembly graph enables us to characterise 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:

$$\emptyset \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\} \xrightarrow{C \text{ invades}} \{A, C\} \quad (1)$$

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

$$\emptyset \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\} \xrightarrow{C \text{ invades}} \{A, C\} \xrightarrow{B \text{ invades}} \{B\} \xrightarrow{A \text{ invades}} \{A\} \quad (2)$$

The sole assumption we make is that invasion rates are much slower than the time it takes for the local dynamics to operate. This means we rule out the scenarios where multiple species invade simultaneously (Lockwood et al. 1997). This assumption offers greater flexibility compared to previous approaches that imposed stricter conditions. For instance, some models mandated that invaders possess low density while the invaded community remains at equilibrium (Serván and Allesina 2021), or that ecological dynamics adhere to deterministic rules with fixed parameters irrespective of arrival orders (Spaak and Schreiber 2023). The framework here transcends these limitations 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. In words, *every ecological assembly can be considered as a walk on the assembly graph*.

### 3 | Ecosystem as an ‘Engine’ of Uncertainty Reduction

Now, you might be thinking, ‘Is not this assembly graph just another way of restating the problem?’ You are right to be sceptical! It is easy to fall into the trap of just relabelling things and calling it progress. However, here is the key distinction: the assembly

graph is deliberately mechanism-agnostic. We are stepping back to look at the assembly process at exactly the right level of abstraction needed to formalise the informational perspective.

We can envision the ecosystem as an engine, processing the 'raw material' of random arrival orders and producing a community with less uncertainty (Margalef 1973; Song, Fukami, and Saavedra 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 us make this concrete. We use the notation  $\dots$  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 is 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 shows 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 is where information theory comes in, specifically Shannon's entropy ( $H$ ):

$$H = \sum_x P(x) \times \log\left(\frac{1}{P(x)}\right) \quad (3)$$

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 would be to see it ('huh, did not 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 us go back to our example with three species (Figure 2g–i). As a null example, we assume that each species has an equal probability of arrival. Then the external uncertainty  $H_{\text{ext}}$ , or the 'messiness' of the species arrival orders, is:

$$H_{\text{ext}} = 6 \times \left(\frac{1}{6} \times \log(6)\right) = \log(6) \quad (4)$$

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

Now, let us look at the internal uncertainty  $H_{\text{int}}$ —the uncertainty in the final community composition. As seen in Figure 2g–i, we have that

$$H_{\text{int}} = \underbrace{\frac{1}{3}\log(3)}_{\{A\}} + \underbrace{\frac{1}{6}\log(6)}_{\{B\}} + \underbrace{\frac{1}{12}\log(12)}_{\{C\}} \quad (5)$$

$$+ \underbrace{\frac{1}{3}\log(3)}_{\{A,C\}} + \underbrace{\frac{1}{12}\log(12)}_{\{B,C\}} = \log(3\sqrt{2})$$

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:  $H_{\text{reduction}} = \frac{H_{\text{int}} - H_{\text{ext}}}{H_{\text{ext}}} \approx -20\%$ . In other words, the ecosystem has 'absorbed' about 20% of the external uncertainty.

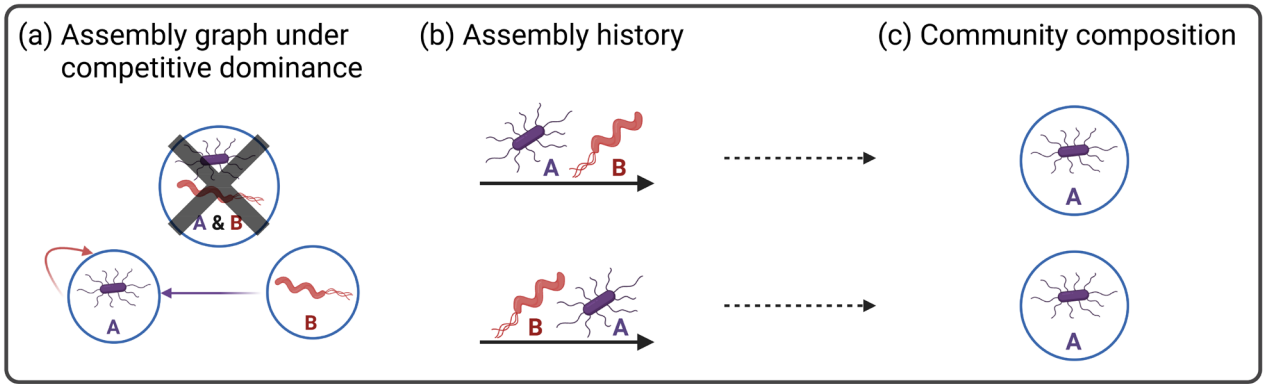
We can even take this analysis down to the level of individual species. Each species within the community might have its own degree of uncertainty reduction. For instance, a species that does not interact much with others, occupying its own niche, would have its uncertainty completely reduced: as long 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 would not have its uncertainty reduced at all—it is unpredictable and at the mercy of chance. To make it concrete, let us consider species  $A$  in our old friend example (Figure 1b) with the same null example of species arrivals (Figure 2g). There are only three equal possibilities for species  $A$ 's arrival (first, second, or last), so the external uncertainty,  $H_{\text{ext}}^A$ , is now  $\log(3)$  instead of  $\log(6)$ . By checking the final compositions with each assembly history (Figure 2h), we see that species  $A$  has a  $2/3$  chance of persistence and a  $1/3$  chance of non-persistence. Using the same formula as before, we can compute the uncertainty reduction for species  $A$ :

$$H_{\text{reduction}}^A = \frac{H_{\text{int}}^A - H_{\text{ext}}^A}{H_{\text{ext}}^A} = \left( \underbrace{\frac{2}{3}\log\left(\frac{3}{2}\right)}_{A \text{ persists}} + \underbrace{\frac{1}{3}\log(3)}_{A \text{ does not persist}} - \underbrace{\log(3)}_{H_{\text{ext}}^A} \right) / \underbrace{\log(3)}_{H_{\text{ext}}^A} \approx -42\% \quad (6)$$

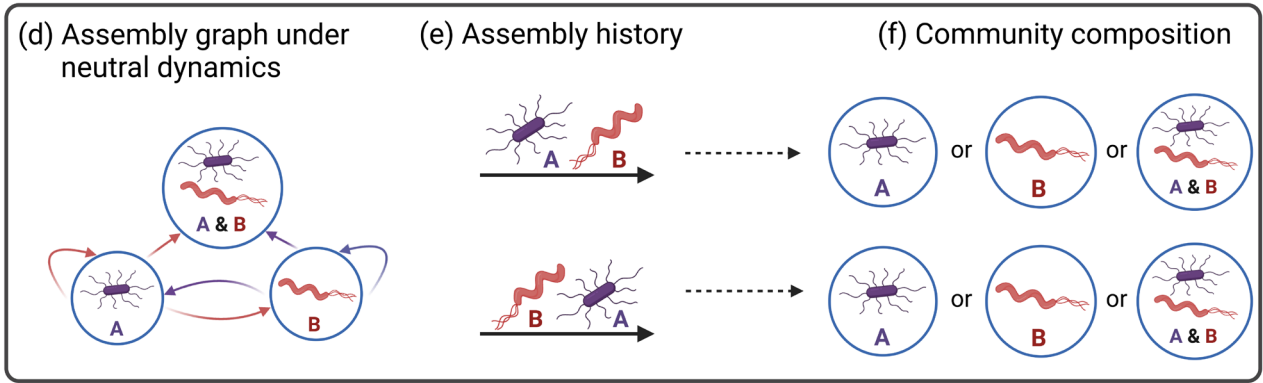
Similarly, for species  $B$  and  $C$ , the relative uncertainty reduction is  $-36\%$  and  $-49\%$ , respectively. Thus, even within the same community, different species can experience different levels of predictability.

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 more realistic assumptions. For example, we can also allow every species to invade more than once (Hewitt and Huxel 2002), or species to arrive with unequal probability due to

Example with uncertainty reduction



Example with uncertainty amplification



Quantifying uncertainty reduction of Figure 1b

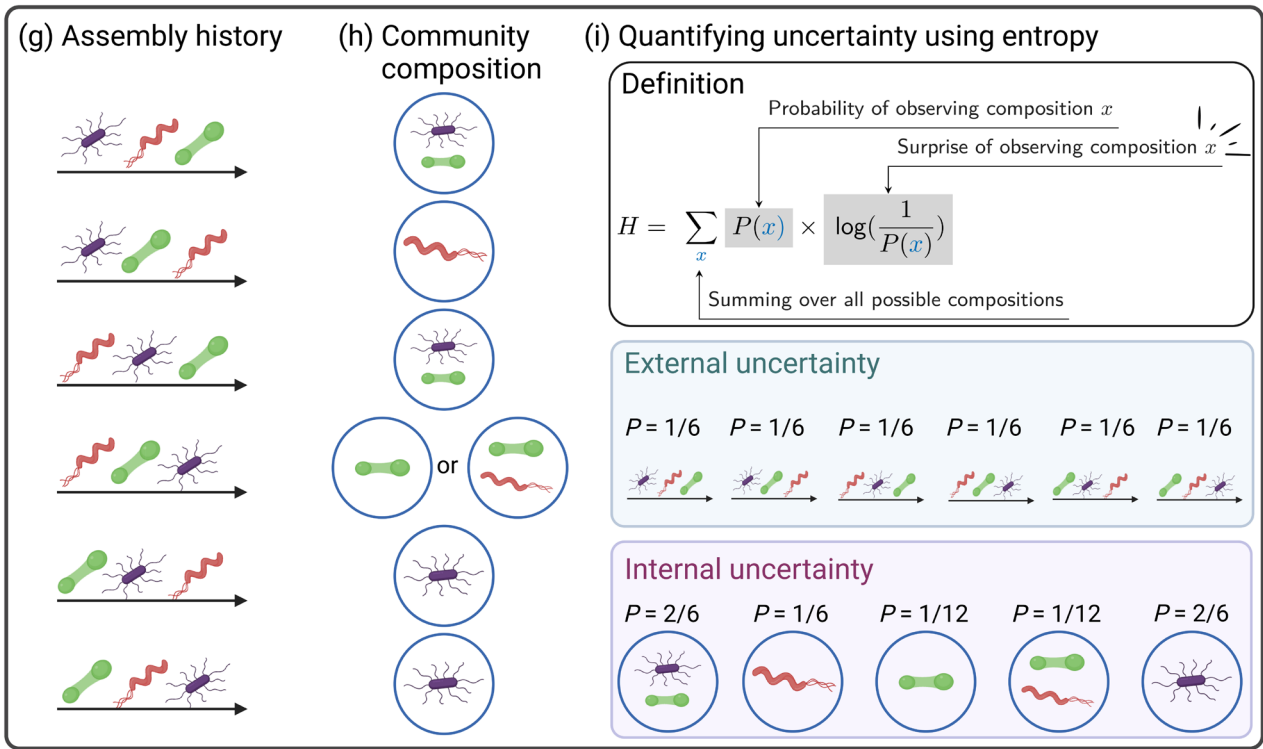


FIGURE 2 | Legend on next page.

seasonality (Zou, Schreiber, and Rudolf 2023) or unequal species abundance (Cingolani et al. 2007).

#### 4 | Breaking It Down: Building Blocks of Community Assembly

By now, you might be thinking, ‘Sure, this assembly graph sounds nifty, but is not it just trading one headache for another?’ And you would be right to wonder. Indeed, as species numbers increase, we are 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 is 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, Fukami, and Saavedra 2021).

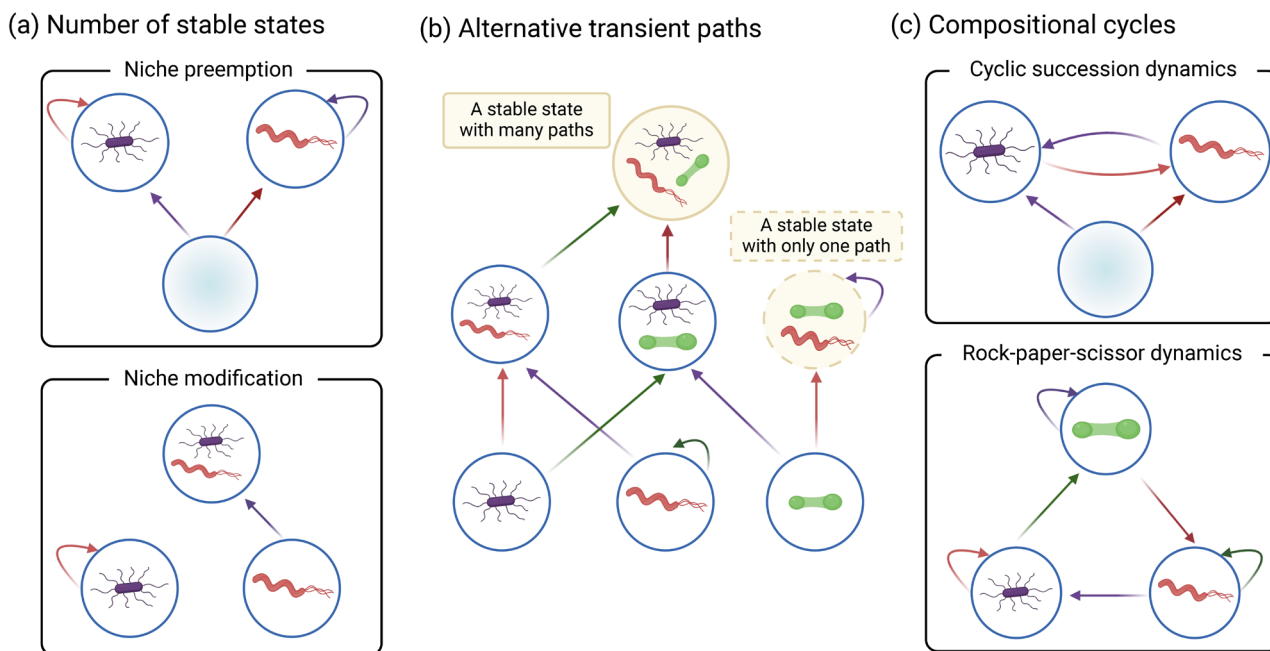
The challenge, then, is to make sense of the labyrinth of complexity. Luckily, we are not the first to grapple with this issue: Interaction networks, where nodes represent species and links represent their interactions, are a cornerstone of community ecology and face similar issues (Montoya, Pimm, and Solé 2006; Coyte, Schluter, and Foster 2015). 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 are not 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 and Morris 2017; Song et al. 2018).

Rather than drowning in the full interaction network, ecologists have long focused on smaller, recurring patterns within networks, known as motifs or modules (Stone, Simberloff, and Artzy-Randrup 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) (Holt 1977; Bonsall and Hassell 1997; Morris, Lewis, and Godfray 2004). These motifs are the ecological equivalent of riffs—they are 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 and 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):

- *Number of Stable States* (Gilpin and Case 1976; Schröder, Persson, and De Roos 2005; Schooler et al. 2011): how many stable compositions a community can settle into. Graphically, it means that the assembly graph has possibly more than one ‘sink’—nodes that have incoming links but no outgoing link (Figure 3a). It is common that a community has only one stable state (climax community) (Clements 1916, 1936). Meanwhile, it is also 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 and 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). It is important to note that the traditional definition of stable states focuses on the long-term, asymptotic behaviour of a system. However, depending on the observation timescale, we may need to consider long transient dynamics, which can persist for extended periods, as another form of stable states (Hastings et al. 2018; Morozov et al. 2020; Arani et al. 2021).
- *Alternative Transient Paths* (Fukami and 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 and 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 and Riley 2004).

**FIGURE 2** | Quantifying uncertainty reduction in ecological assembly. The top row presents a case of complete uncertainty reduction under competitive dominance, where two possible species arrival orders (panel b) converge to a single final community composition (panel c) through an assembly graph (panel a) with species *A* competitively excluding species *B*. The middle row demonstrates uncertainty amplification under neutral dynamics (panel d), where two arrival orders (panel e) lead to three equiprobable community compositions (panel f) via an assembly graph (panel e) lacking competitive interactions. The bottom row 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.



**FIGURE 3** | Assembly motifs as building blocks of assembly graph. This figure illustrates three common assembly motifs found in ecological assembly. Panel (a) shows the number of 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 monopolise 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 compositional 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*).

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 is like predicting where skiers end up: if all trails lead to the same lodge (i.e., no alternative stable states), it is 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), prediction becomes easier. Looping trails (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, Fukami, and Saavedra 2021). Importantly, we need all four of them. Historically, most attention has been paid to the number of stable states (Schröder, Persson, and De Roos 2005; Abreu et al. 2020; Amor, Ratzke, and Gore 2020). But, especially in small communities, the other three motifs can play an even bigger role in reducing uncertainty than the number of stable states (Song, Fukami, and Saavedra 2021).

## 5 | 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 (MacArthur and Levins 1967; Armstrong and McGehee 1980; Grainger, Levine, and Gilbert 2019). In essence, we begin with a resident community at equilibrium and then introduce a new species at low density. For instance, if we are 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’. Traditional metrics, such as local/global stability (the ability of a community to return to equilibrium after a small/large disturbance), can be overly restrictive. These concepts essentially 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 will not vanish 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 characterise natural communities

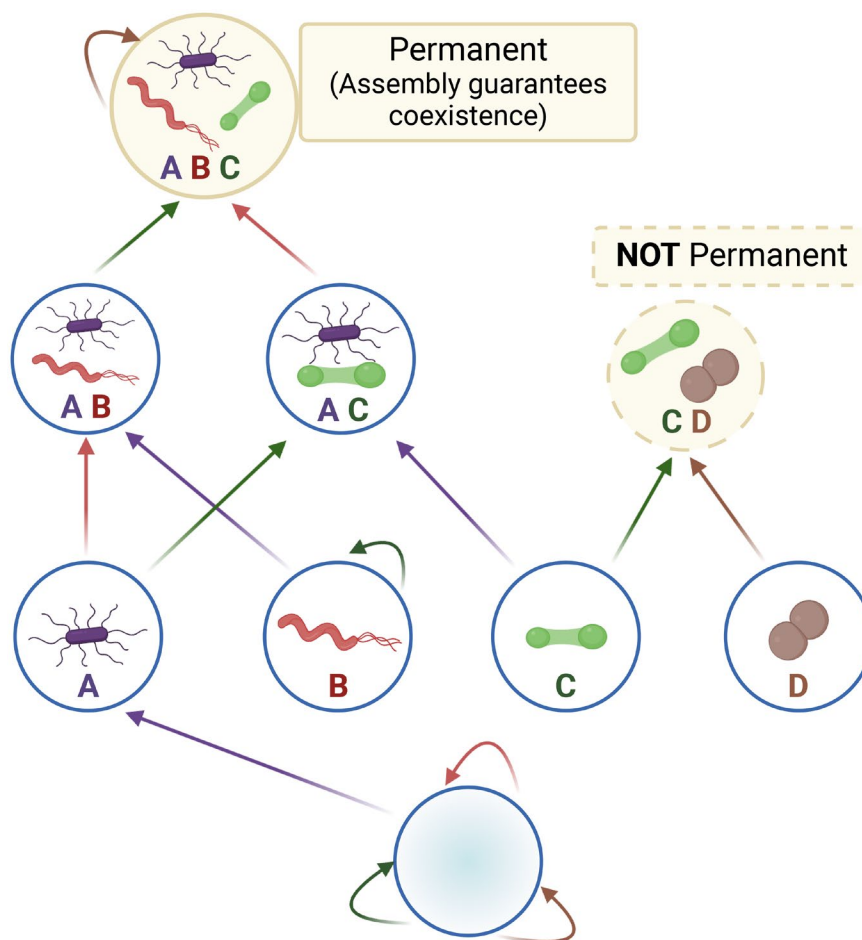
(Pennekamp et al. 2019; Rogers, Johnson, and Munch 2022), while treating traditional metrics like global stability as merely a special case. Therefore, permanence is a more natural and meaningful way to define coexistence.

However, permanence is less used because it is typically difficult to verify. Surprisingly, it turns out there is a simple way to figure out if a community is permanent, just by looking at its assembly graph. Here we briefly review this exciting recent advance in the mathematical theory of permanence (Hofbauer and Schreiber 2022; Spaak and Schreiber 2023; Almaraz et al. 2024). There are two conditions that need to be met for this method to work. First, the assembly graph must be acyclic, meaning it lacks cyclical patterns of community assembly (i.e., absence of compositional cycles). Second, if a community composition has multiple equilibria, then an invading species into this composition must be able to establish under all equilibria or under none (consistency of invasibility across equilibria). If these two conditions hold—and they often do—then a community is permanent *if and only if* each of its coexisting subcommunities can be invaded by at least one species. This criterion is not a mere rule of thumb, as traditional invasion

criteria have unfortunately been (MacArthur and Levins 1967; Grainger, Levine, and Gilbert 2019); it is rigorously proven.

The beauty of this criterion lies in its visual clarity and ease of application. Let us illustrate with the assembly graph in Figure 4. First, we confirm it is 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:  $\emptyset$ ,  $\{A\}$ ,  $\{B\}$ ,  $\{C\}$ ,  $\{A, B\}$ ,  $\{A, C\}$ . Note that we omit  $\{B, C\}$  because *B* and *C* cannot coexist without *A*. 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 within species pool *A*, *B*, and *C*.

In contrast, for the other stable state  $\{C, D\}$ , while the subcommunities  $\{C\}$  and  $\{D\}$  can be invaded, the empty community  $\emptyset$  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



**FIGURE 4** | Graphical criterion for 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  $\emptyset$  cannot be invaded, potentially due to an Allee effect where neither species (*C*) nor species (*D*) can establish at low densities. This violates the criterion, which requires all subcommunities (including the empty community) to be invadable by at least one species from the pool (species *C* and *D*).



and launch a coordinated attack, making it difficult to establish (Moreno-Gómez et al. 2017; Weiser, Ferreira, and Paton 2018).

This graphical criterion almost seems too good to be true. It is 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 were not enough, it also ties in with Modern Coexistence Theory, a leading framework for studying species coexistence, which is built upon invasion criterion (Chesson 2000; Barabás, D'Andrea, and Stump 2018; Song, Barabás, and Saavedra 2019). Modern Coexistence Theory has gained widespread acceptance among empirical ecologists studying community assembly (HilleRisLambers et al. 2012; Kraft and 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 (Barabás, D'Andrea, and Stump 2018; Pande et al. 2020; Arnoldi et al. 2022). The new theory (Hofbauer

than others, simply because their interaction structures (who interacts with whom and how strongly) are compatible 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 quantities 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 quantity, 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 quantity, 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 is 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  $\mathbf{X}$  to composition  $\mathbf{Y}$ , the probability is simply proportional to (Long et al. 2024):

$$P(\mathbf{X} \rightarrow \mathbf{Y}) \propto \frac{\Omega_{\mathbf{Y}}}{D_{\mathbf{X},\mathbf{Y}}} \quad (7)$$

↑ Transition probability from composition  $\mathbf{X}$  to  $\mathbf{Y}$ 
↑ Probability of  $\mathbf{Y}$  coexistent

↑ Dissimilarity between compatible environments

and Schreiber 2022; Spaak and Schreiber 2023; Almaraz et al. 2024) 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

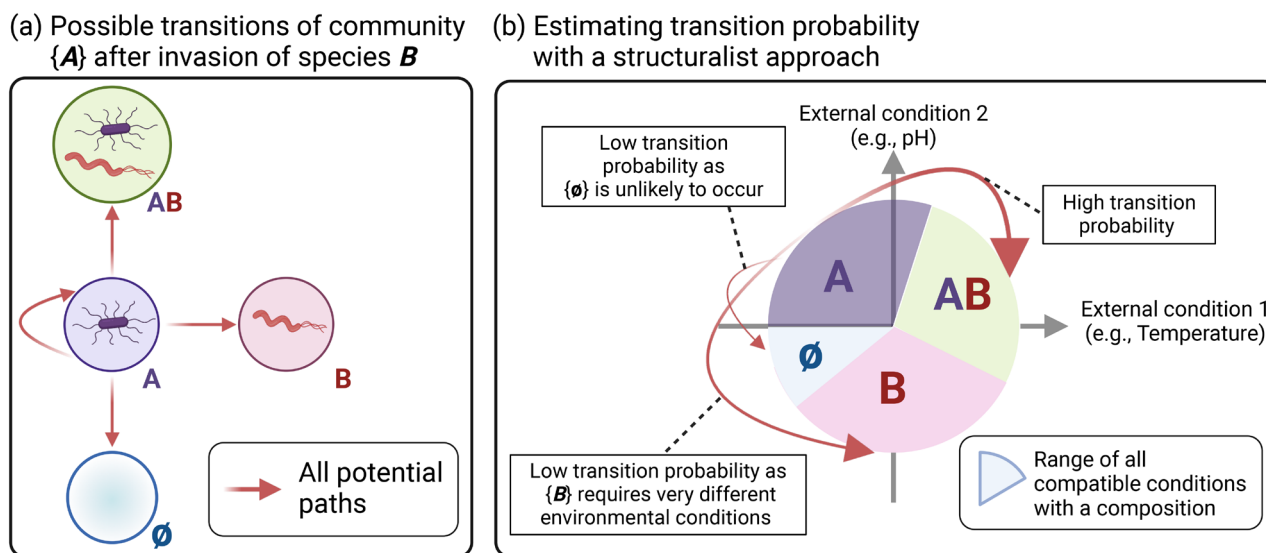
So far, all the links in our assembly graph have been binary—either a transition between states is possible or it is not. But nature rarely deals in such absolutes. The ecological dynamics underlying assembly might be inherently random (Obadia et al. 2017; Vega and Gore 2017). The environment, too, is a maelstrom of change, with shifts in temperature or resource availability (Jones et al. 2022; Debray 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 two approaches. The first approach is a matter of statistical rigour, to acknowledge that our models and data are imperfect and to quantify the errors inherent in our analyses (Terry and Armitage 2024). This kind of statistical rigour is increasingly becoming the norm in the field (Bowler et al. 2022; Hess et al. 2022; Majer et al. 2024).

But there is another, complementary approach, one that seeks to estimate uncertainty based on the structure of the ecological community itself (Alberch 1989; Gould 2002). The idea is that some communities are inherently more likely to occur

To illustrate, consider a simple community with only species  $A$ , and then species  $B$  attempts to invade (Figure 5a). There are several possible outcomes: the community could become empty  $\emptyset$  (e.g., due to the enrichment paradox, where increasing resources can paradoxically lead to extinction, see Roy and Chattopadhyay 2007),  $B$  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 outcomes has a different probability (Figure 5b). For example, the transition from  $\{A\}$  to the empty community  $\emptyset$  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.,  $\Omega_{\{\emptyset\}}$  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  $D_{\{A\},\{A,B\}}$ ).

This approach has already shown promise in understanding the probabilistic assembly across a wide range of empirical ecosystems (Long et al. 2024; Deng et al. 2024; Godoy et al. 2024). For example, it explains why and when microbial communities can switch across few dominant communities (Long et al. 2024; Ogbunugafo and Yitbarek 2024). For another example, it explains how environmental changes across years constrain assembly paths in annual grass communities (Godoy et al. 2024).



**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  $\Omega_Y$ ), 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  $\Omega_Y$ ) 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.

In essence, the probabilistic approach allows us to quantify our ignorance. We acknowledge that we do not have perfect knowledge of the system, but we use the information we do have (Figure 5b) to make informed predictions about its future. It is a way of embracing uncertainty, not as a roadblock, but as an integral part of the ecological puzzle.

## 7 | Linking Class of Ecological Models and Topology of Assembly Graphs

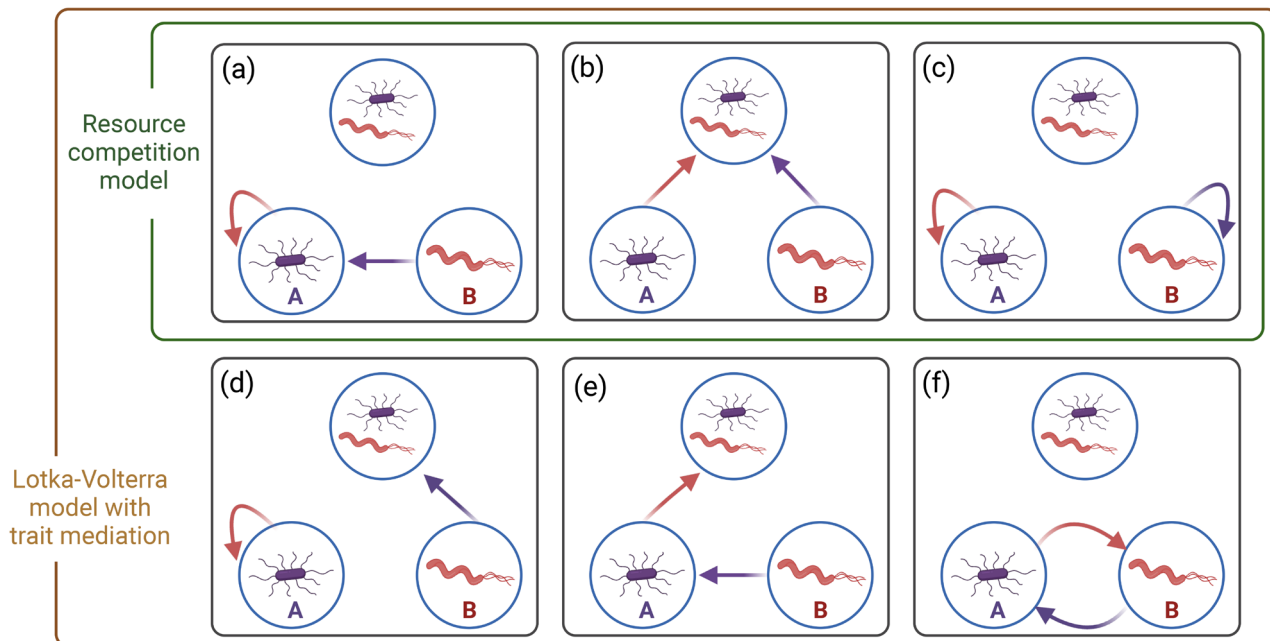
So far, we have studied the assembly graph in its most general form and not restricted ourselves to any particular ecological dynamical model. But, like any good tool, it is even more useful when you have the right attachment for the job. In ecology, that attachment is the specific dynamical model—the rules it lays out for how species interact. The specific *class* of an ecological model, by which we mean the form of the equations and the way species interactions are represented, 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 is like the model's DNA is written into the graph's shape.

To illustrate, let us take a classic example of two species competing for resources with MacArthur-type dynamics, a standard mechanistic model in ecology (MacArthur 1969; Tilman 1982; Sakarchi and Germain 2024). 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 does not matter;

Figure 6b), or whoever gets there first takes all (Figure 6c). That is 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 would be absolutely right. The simple models we have explored so far assume that species interactions are fixed. But in reality, the way species affect each other can often depend on who arrived first. 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 is an example of a *trait-mediated* priority effect—the ability of a species to consume resources depends not only on its own traits, but also on the traits of the species already present (Rudolf 2019). To capture this complexity, we need to expand our model class. By incorporating trait-mediated priority effects, we can account for a wider range of ecological interactions and generate three other possible topologies of assembly graphs (Figure 6d–f) (Zou, Yan, and Rudolf 2024). These six topologies exhaust all possible assembly graphs with two competing species (Song, Fukami, and Saavedra 2021).

Two species are easy to wrap our heads around, but what happens with more species? Theoretical ecologists, as Robert May put it, 'count like the Australian Arunta tribe, "one, two, many," and move on [...] directly to multi-species communities'



**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). The ecological scenario of panel (d) is discussed in the main text. The ecological scenario of panel (d) is discussed in the main text. Panel (e) shows a scenario where coexistence requires one species to establish first but not the other one. This scenario can happen with asymmetric niche modification of the environment among species. Panel (f) shows a scenario where each species is competitively advantageous to the other only when it is at low abundance. This scenario can happen with maladaptation, where the fitness of a species decreases in its current environment (Crespi 2000).

(May 1976). Luckily, recent work has made real progress in understanding three-species competition systems (Lee, Bloxham, and Gore 2023; Ranjan, Koffel, and Klausmeier 2024). They have 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) (Friedman, Higgins, and Gore 2017), MacArthur resource competition model (Tilman 1982), 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 categorisation 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, called ‘coexistence holes’ (Letten 2021; Angulo et al. 2021). In a rough analogy, assembly holes tell us how ‘continuous’ the assembly process is. For example, if any single species and any pair of species can persist, but the triplet cannot, then the assembly is not continuous. Counting these coexistence holes has already led to some exciting progress in classifying how communities assemble (Flores-Arguedas et al. 2023).

Another approach is to move beyond specific models and instead explore the *typical* behaviour of diverse communities. This involves using established models with randomised parameters for species interactions—an approach with a rich history in ecology (May 1972; Bunin 2017). Here, ‘typical behaviour’ refers to the most likely patterns of community assembly that emerge despite the randomness in the specific interactions. For example, how many species typically coexist? How much variation is there in the final community composition? 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). Another 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 and Allesina 2021). While the approach of random interactions might seem purely theoretical, recent empirical work suggests it can be a surprisingly useful tool for understanding complex microbial communities (Dal Bello et al. 2021; Hu et al. 2022; Moran and Tikhonov 2022).

In sum, there exists a direct correspondence between the *class of ecological models* and the possible *topologies of assembly graphs*. Models provide detailed understanding of ecological mechanisms at play, but they can be hard to figure out from real-world data (Angulo et al. 2017; Remien, Eckwright, and Ridenhour 2021; Nguyen, Rohr, and pomati 2024). In contrast, assembly graphs are directly observable, but they do not

inherently reveal the underlying ecological mechanisms driving those pathways. The beauty of this correspondence is that models and graphs are actually a dynamic duo that complement each other. For example, we can use the topology of the assembly graph to tell us if the very class 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, Law, and Weatherby (2003). Why the scarcity? First, ecologists might not yet fully appreciate the potential of this emerging tool, often favouring established ‘the tried and true’ methods over the new kid on the block. Second, and more importantly, doing the actual experiments is *hard*. It is 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 and Rudolf 2023). While I clearly lack expertise in experimental ecology, I would 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. Some notable examples include: deep-learning methods (Baranwal et al. 2022; Michel-Mata et al. 2022; Wu et al. 2024); Bayesian statistics, which can incorporate prior knowledge and uncertainty into the inference process (Maynard, Miller, and Allesina 2020; Skwara et al. 2023; Lemos-Costa, Miller, and Allesina 2023); and compressive sensing, which can accurately reconstruct sparse signals from limited measurements (Arya, George, and O’Dwyer 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, emphasising 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 (Tian et al. 2020; Louca et al. 2018; Goldford et al. 2018). And there is even evidence suggesting that the effects of a species on community function might simply be additive (Diaz-Colunga et al. 2023, 2024; Ardell et al. 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 and 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 is far from a finished book. Many chapters remain unwritten, and some of the most exciting stories may lie in the unexplored corners. Here, I will highlight three promising research directions that are extremely important but less travelled.

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 cannot 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 an invasion attempt by Harald Hardrada of Norway in the same year. This phenomenon is not just theoretical musing. Empirical work has already 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 (Benson, Gleich, and Leskovec 2016; Ferraz de Arruda, Aleta, and Moreno 2024), 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, Fortin, and Gonzalez 2022) and climate change (Baldrian, López-Mondéjar, and Kohout 2023; van Klink et al. 2024). Importantly, disassembly is not simply assembly in reverse; it operates under its own set of ecological principles and requires the development of new theoretical frameworks (He and Hubbell 2011; Storch, Keil, and Jetz 2012). It is like a game of Jenga—extracting blocks (species) from an existing tower involves a different strategy than building it up. For example, in the gut microbiome, removing pathogens (disassembly) requires different strategies, like targeted antibiotics, than introducing beneficial microbes (assembly), such as probiotics. 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 unravelling the corresponding mechanisms that govern disassembly (Torres, Kuebbing, et al. 2024; Torres, Morán-López, et al. 2024). For another example, the concept of

‘assembly holes’, which are 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.

The third direction concerns multiple equilibrium abundances. In this paper, multiple stable states are defined as different sets of coexisting species. However, multiple stable states in the literature are also used to describe scenarios where the same set of species can coexist at different equilibrium abundances (AlAdwani and Saavedra 2019; Ben Arous, Fyodorov, and Khoruzhenko 2021). For example, in a community with two species, one species may have a higher abundance than the other at one equilibrium and vice versa at another equilibrium. An emerging line of work on multiple equilibrium abundances studies the basins of attraction for each equilibrium, which represent the range of initial conditions that will lead to each equilibrium (Menck et al. 2013; Advani, Bunin, and Mehta 2018; Zhang et al. 2024). This direction may naturally bridge the dynamical approach and the probabilistic approach, with the probability now stemming from which equilibrium the community is at.

## 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 centre 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’ (Schrödinger 1946), has already proven valuable in guiding the development of biophysics (Avery 2021; Jeffery, Pollack, and Rovelli 2019). The information perspective is both conceptually intuitive and computationally feasible, providing a mechanism-agnostic umbrella to other approaches. This perspective might be particularly relevant in today’s world. We are witnessing not just shifts in average conditions, but alarming increases in variability (Bathiany et al. 2018; Seddon et al. 2016). Recent studies suggest this volatility might be even more detrimental than the changes in means (Vasseur et al. 2014; Ma, Ma, and Pincebourde 2021). It is not far-fetched to hypothesise that ecosystems are pushed beyond their capacity to ‘absorb’ the external uncertainty (Chesson 2017; Wolkovich and Donahue 2021). This idea needs to be tested rigorously, of course, but it hopefully provides some food for thought.

With the information perspective as a foundation, we can construct dynamical and probabilistic theories, and connect past theories to this new framework. I have 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 (van den Berg et al. 2022).

The assembly graph is a tool, not a panacea. It raises many questions (hopefully fewer than the questions it answers). Its applicability to diverse ecological systems remains to be fully explored. Recent advancements in microbial ecology provide an ideal testing ground for ecological assembly and offering new insights into this long-standing problem. 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 specialised 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 encyclopaedia of ecological assembly theory. I am also not saying the assembly graph is the definitive way to go forward—there is ample room for debate—but it presents an exciting opportunity to test and refine our understanding of assembly. 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 captivating world of ecological assembly.

### Author Contributions

**Chuliang Song:** conceptualization (lead), investigation (lead), investigation (lead), project administration (lead), project administration (lead), project administration (lead), visualization (lead), visualization (lead), visualization (lead), writing – original draft (lead), writing – original draft (lead), writing – original draft (lead), writing – review and editing (lead), writing – review and editing (lead), writing – review and editing (lead).

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The author declares no conflicts of interest.

### Data Availability Statement

The author has nothing to report.

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