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Toward a Conceptual Commons for Theory in Community Ecology

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Abstract

Community ecology has developed a rich and increasingly diverse body of theory, but its rapid expansion has outpaced efforts to compare and synthesize competing frameworks. As a result, semantic ambiguity often masks genuine scientific disagreement. Using theories of species interactions as a lens, I organize this landscape along two axes: formalization (how theories are built) and function (why they are used). Within formalization, I contrast the model-driven culture (which imposes structure) with the data-driven culture (which discovers it), highlighting the distinct forms of misspecification that plague each. Within function, I distinguish three goals: building predictive heuristics, developing definitional frameworks, and running experiments in model worlds. I use this mapping to identify where and why distinct traditions talk past one another, drawing on examples from modern coexistence theory, diversity–stability relationships, niche theory, and network ecology. This analysis provides a diagnostic roadmap for pinpointing why models disagree, justifying the choice of formalization, and aligning questions with appropriate theoretical tools. Beyond diagnosis, I survey current integration efforts and outline practical steps toward synthesis. Finally, I address the human dimension of theoretical practice, arguing that artificial intelligence offers a major opportunity to democratize access to theory if training pivots from derivation to verification. This review lays the groundwork for a conceptual commons where diverse theories can be rigorously compared and productively combined.

1. INTRODUCTION: ECOLOGY'S BABEL PROBLEM

[O]ur truth is the intersection of independent lies.

—Richard Levins (1966)

Interaction strength: a generic label for how strongly one species affects another's growth; in practice, it is measured in many nonequivalent ways

Ecological stability: an umbrella term for a system's tendency to persist or recover; like interaction strength, it is defined and measured in many different ways across theories

Niche: the set of environmental conditions and resources that allow a species to persist; defined and measured in many competing ways

Formalization: how we turn an ecological system into a specific set of equations or algorithms

Function: the main job a theory is built to do: predict, define, or explore "what ifs"

Lotka–Volterra equations: a foundational family of differential equations that model population dynamics through pairwise species interactions

Few sciences are as stubbornly empirical as ecology, and few have built as ambitious a body of theory. Starting from the foundational population models in the early twentieth century (Scudo & Ziegler 1978), ecologists have relied on theories not as optional embellishments but as central tools for making sense of nature's "entangled bank" (Darwin 1859). Compared with many other fields of life science, ecology has maintained a particularly tight feedback between theory and empiricism: Theoretical ideas motivate experiments, experimental results reshape theories, and this reciprocal interplay has been one of ecology's greatest strengths (Kingsland 1995, Marquet et al. 2014).

Over the last few decades, the landscape of ecological theory has changed dramatically. The field is witnessing an explosion of theoretical approaches, driven by a combination of factors: the proliferation of computational power, the rise of large-scale observational and experimental data sets (Hampton et al. 2013), and the import of methods from other fields such as physics (Meron 2015, Azaele et al. 2016, Cui et al. 2024) and economics (Archetti et al. 2011, Frank & Sudarshan 2024). Ecological theories use everything from differential equations and individual-based simulations (Grimm & Railsback 2005) to multivariate time-series methods (Ives et al. 2003, Medeiros et al. 2025) and deep learning (Christin et al. 2019, Borowiec et al. 2022, Han et al. 2023). This diversity is intrinsically valuable, as the variety of fundamental and applied ecological questions demands a rich theoretical toolkit.

At the same time, the sheer speed of this expansion has birthed a Babel problem: a growing conceptual fragmentation where the field's vocabulary has failed to keep pace with its methodological diversity (Herrando-Pérez et al. 2012, Trombley & Cottenie 2019). Researchers increasingly apply identical labels—interaction strength, ecological stability, niche; the list goes on—to mathematical quantities that differ fundamentally in their units, assumptions, and scales. This semantic overload creates a dangerous ambiguity: It masks the fact that distinct frameworks are often measuring incomparable things. Consequently, it becomes difficult to synthesize progress or to distinguish genuine scientific contradictions from artifacts of definition. Too often, what appears to be a deep disagreement about the nature of an ecosystem is, in reality, a misunderstanding of a model's structure or its intended function.

This review arises from that tension. Rather than a grand unifying theory, what ecology needs is a conceptual commons—functioning conversations across many imperfect theories, where diverse frameworks can be rigorously compared and productively combined. I do not attempt to construct such a monolithic theory or to exhaustively harmonize all subfields. Instead, my aim is diagnostic. I map the apparent fragmentation along two underarticulated dimensions: formalization (how we encode ecological systems into mathematical or algorithmic structures) and function (why we build particular models and what we expect them to do: prediction, definition, and experiment). Within each dimension, I examine the underlying philosophies, diagnose recurring sources of confusion, and outline concrete pathways for integration. Given the vast scope of the literature, I highlight key existing syntheses that address specific aspects of this landscape; this selection serves not as an exhaustive census but rather as a curated guide to the state of the art, acknowledging that many deserving publications could not be included.

I use the theories of species interactions as a vehicle for these ideas. This is a deliberate choice. Among the subfields of ecology, the study of species interactions is arguably the most mathematically diverse: from Lotka–Volterra equations to machine learning classifiers, from coexistence

theory to network analysis. It is also the arena where cross-framework debates have been most intense and most instructive. As such, it serves as an ideal lens with which to diagnose the broader theoretical challenges that confront ecology as a whole. I draw on a wide range of theoretical traditions—from modern coexistence theory to diversity–stability relationships, and from niche theory to network ecology—to develop these lessons, which apply well beyond species interactions to ecology at large.

Misspecification: situation where a model's assumed structure does not match the actual process generating the data

The remainder of this review is organized as follows. I examine the dimension of formalization in Section 2, distinguishing between model-driven and data-driven cultures. In Section 3, I propose strategies to mitigate the specific forms of misspecification that plague each approach. I then turn to the dimension of function in Section 4, categorizing theoretical frameworks into predictive heuristics (prediction), definitional frameworks (definition), and theoretical experiments (experiment). Section 5 shows how mismatches in these functions lead to unproductive debate and outlines pathways to synthesize each of them. Finally, Section 6 discusses the human dimension of theoretical practice—addressing how education, software tools, and the growing role of artificial intelligence (AI) must evolve to support this conceptual coherence.

2. BUILDING BLOCKS: THE TWO CULTURES OF FORMALIZING SPECIES INTERACTIONS

> What we observe is not nature in itself, but nature exposed to our method of questioning.
>
> —Werner Heisenberg (1958)

Every ecological model is a choice (Levins 1966, Trappes 2024). Even before a single equation is written or an algorithm is coded, the modeler has implicitly committed to a set of decisions about what matters (Scheiner et al. 2025): which entities to represent, which processes to include, and at what scales to operate. This is formalizing, the act of choosing a specific way to encode assumptions, data, and hypotheses. These choices are never neutral transcriptions of nature; rather, they serve as a lens that strictly delimits which patterns are visible and which questions are answerable.

Crucially, these choices are often inherited rather than intentional. Different subfields gravitate toward different default formalizations, which are sometimes so deeply ingrained that they become invisible to practitioners. A predator–prey system, for instance, might be formalized as a pair of Lotka–Volterra equations, as a spatially explicit individual-based model, or as a high-dimensional autoregressive process inferred from time series—yet all three are ostensibly about the same ecological system.

Formalization choices can be classified along many axes. One might focus on mathematical structure—continuous versus discrete, deterministic versus stochastic—yet these distinctions often concern the dialect of mathematics more than the representation of biology. Alternatively, one might look to the classic mechanistic–phenomenological divide, but these labels are notoriously slippery; one researcher's "mechanism" is often another's "phenomenology." Instead, I adopt a lens inspired by Leo Breiman's (2001) seminal essay on the "two cultures" of statistical modeling. Breiman contrasted a data modeling culture, which assumes that observations are generated by a specified probabilistic model, with an algorithmic culture, which treats nature as a black box and uses flexible algorithms primarily for prediction. This dichotomy mirrors recent debates in ecology regarding the role of forecasting, often framed as a trade-off between predictive ecology and explanatory understanding (Mouquet et al. 2015, Dietze 2017, Houlahan et al. 2017, Hendry 2023).

Structure: specific mathematical or algorithmic architecture that encodes the relationships between ecological entities

For the purposes of this review, however, this mapping is not exact. In ecological theory, the boundary between explanation and prediction is blurred; many approaches that appear algorithmic are routinely used for explanation and mechanism building. I therefore rephrase the distinction in terms of two cultures of formalization: a model-driven culture and a data-driven culture. The defining difference is the origin of structure. In the model-driven culture, structure is imposed a priori: An explicit process model is derived from biological principles, and data are used to parameterize and test it. In the data-driven culture, structure is discovered a posteriori: Flexible algorithms are fitted to observations with minimal prior commitments, allowing interaction patterns to be learned from the data themselves. While both cultures rely on models and data, this contrast—between imposing structure and discovering it—captures a fundamental divide in how ecologists formalize nature.

2.1. Culture 1: Model-Driven Formalization

The model-driven culture is the traditional stronghold of theoretical ecology. Its core philosophy posits that nature's complexity can be distilled into an underlying mathematical structure representing the key processes driving interactions. Practitioners typically regard these models as "caricatures"—knowingly incomplete, but valuable precisely because they isolate the aspects of the system deemed most relevant for the questions at hand (Levins 1966). In this culture, the ecological "story" is articulated first, in terms of entities, mechanisms, and causal flows; the formal model is then built to encode that story.

Model-driven formalization encompasses the classics of the field: population-level models such as Lotka–Volterra systems, consumer–resource dynamics (Wangersky 1978), and their extensions involving higher-order interactions (Gibbs et al. 2022), eco-evolutionary processes (Abrams 2000, Bell 2017, Hendry et al. 2018), or network structure (Bascompte & Jordano 2007, Guimaraes 2020). It also includes individual-based and agent-based models, which, despite tracking discrete organisms, rely on explicit, prespecified rules governing behavior and movement (DeAngelis & Mooij 2005). Even statistical frameworks fall under this umbrella when they are used to test specific mechanistic hypotheses—for instance, fitting a hierarchical model whose functional form is strictly dictated by demographic assumptions rather than chosen for pure predictive flexibility (King 2014).

The primary strength of the model-driven culture is its explanatory leverage. By making assumptions explicit, these models allow researchers to explore the logical consequences of biological ideas, derive analytical conditions for coexistence, and search for general principles that hold across systems. They serve as logical laboratories: Even when they do not perfectly match a specific empirical system, they clarify the set of possibilities.

However, the conclusions depend on the structural choices made at the outset. These choices, once fixed, determine what the model can and cannot see. The risks of this dependency are not hypothetical. In an application of plant–soil feedback theory, a parameterized model predicted that a particular three-species community could not coexist (Kulmatiski et al. 2011). Subsequent theoretical auditing revealed that this was not a biological property of the community but rather a mathematical artifact of the canonical framework, which structurally precludes stable coexistence for more than two species regardless of parameter values (Miller et al. 2022). Similarly, fluctuation-dependent coexistence mechanisms, such as relative nonlinearity, mathematically require nonlinear responses to variation (Chesson 2000). If empiricists analyze environmental fluctuations by using ecological models that are linear by construction, conclusions about these mechanisms are ruled out a priori by the model structure (Barabás et al. 2018). These cases underscore a fundamental tension in model-driven formalization: The very structure that enables insight can also silently foreclose biological possibilities.

2.2. Culture 2: Data-Driven Formalization

The data-driven culture starts from the opposite pole. Here, ecological systems are treated as high-dimensional, partly unknown, or effectively a black box. Rather than committing at the outset to a detailed process model, the practitioner specifies a flexible statistical or algorithmic architecture and allows the data to determine the effective structure. Patterns, forecasts, and interaction networks are learned from observations with minimal mechanistic constraints. In this culture, structure is discovered rather than assumed.

Data-driven formalization is defined not by the novelty of the data but by how the data are used. Quadrat sampling, natural-history observations, species censuses, and long-term monitoring programs can all support data-driven formalization if they are analyzed with methods that infer structure from observations rather than impose a prespecified process model. A decades-long bird census is therefore no less capable of supporting a data-driven analysis than an environmental DNA survey; the distinction lies in the analytical posture, not the technological source of the measurements. What has changed in recent years are the scale and heterogeneity of available observations. High-throughput sequencing and environmental DNA now allow the reconstruction of diets and food webs at resolutions that were previously unattainable (Cristescu & Hebert 2018, Pringle & Hutchinson 2020, Miya 2022). Computer vision and deep learning applied to camera traps and satellite imagery provide systematic data on co-occurrence and habitat use across vast scales (Bjerge et al. 2022, Blair et al. 2024). Long-term observatories such as the National Ecological Observatory Network (NEON) generate standardized, multivariate time series across broad spatial and taxonomic gradients. Such data streams are often rich, heterogeneous, and only indirectly aligned with the state variables of classical theory. They therefore intensify the appeal of flexible methods that can map high-dimensional observations to ecological outputs without first specifying all underlying mechanisms.

Within this culture, I distinguish two broad modes. The first aligns closely with Breiman's (2001) "algorithmic culture," where success is measured primarily by predictive performance. Here, the goal is to build accurate mappings from covariates to outcomes, with interpretability often secondary. Machine learning models are employed to predict species interactions on the basis of traits and phylogeny (Pichler et al. 2020, Pereira et al. 2023, Biton et al. 2025) or to forecast population trajectories (Ushio & Kawatsu 2020). In this mode, a model is validated by its ability to generalize to out-of-sample data, irrespective of whether its internal representation resembles a known biological process (Breiman 2001, Houlahan et al. 2017).

Crucially, however, the rise of data-driven methods in ecology has not signaled a retreat from explanation. This marks the second, distinctively ecological mode: the use of flexible algorithms for causal discovery and causal inference. Approaches such as empirical dynamic modeling exemplify this ambition (Chang et al. 2017, Munch et al. 2023a, Edwards et al. 2024): Convergent cross mapping is used to detect the presence of directional coupling (discovery) (Sugihara et al. 2012), while state-dependent mappings (S-maps) estimate time-varying coefficients to quantify interaction strengths (inference) (Ushio et al. 2018). This trend is accelerating, as evidenced by the publication of at least five major reviews on ecological causal inference in the past year alone (Byrnes & Dee 2025, Correia et al. 2025, Franks et al. 2025, Schrodt et al. 2025, Siegel & Dee 2025), alongside a growing—albeit more nascent—focus on causal discovery (Song et al. 2022, Bouwman 2024).

Consequently, the data-driven culture has generated a dual mandate wherein models serve simultaneously as predictive engines and mechanistic lenses. Algorithms are increasingly interrogated for biological insight, with internal metrics—variable-importance scores, network structures, or state-dependent coefficients—interpreted as proxies for process. Yet this conflation

Causal discovery: refers to algorithms that analyze data to determine which variables drive others, identifying causal links without prior assumptions

Causal inference: refers to statistical methods to estimate the strength of an effect (e.g., predation) when the causal link is already assumed to exist

Empirical dynamic modeling: refers to time-series methods that reconstruct system dynamics directly from data instead of specifying explicit equations

Convergent cross mapping: a time-series method that tests whether information about one variable is encoded in the dynamics of another, providing evidence of directional causal coupling

State-dependent mapping (S-map): a time-series method that estimates how the relationship between species changes with the system's current state

drives conceptual fragmentation, as the assumptions required to optimize a forecast do not necessarily support the causal narratives built upon them.

2.3. The Twin Risks: Misspecification and Semantic Ambiguity

The model-driven and data-driven cultures differ in how they build structure, but they share inherent vulnerabilities. Formalizing ecological intuition into rigid mathematics or code forces commitments that expose the researcher to two distinct risks: either that the structure is wrong or that the structure redefines the question in ways we do not realize.

The first risk is misspecification: the danger that the imposed model does not match the actual data-generating process. In the model-driven culture, this is the cost of mathematical precision. To build a model, the researcher must select from a vast dictionary of plausible components—forms of density dependence, dispersal kernels, noise colors—with only limited empirical guidance. Different, equally defensible structural choices can lead to radically different narratives about system behavior (Wood & Thomas 1999). In the data-driven culture, this mismatch appears when the algorithm's implicit assumptions violate the system's reality (Yates et al. 2018). Nonstationary dynamics may be treated as stationary; latent variables may violate independence assumptions. The belief that such methods are assumption-free or model-free does not eliminate these structural commitments; it simply makes them harder to detect.

The forms of misspecification differ, but the consequences rhyme. A mechanistic model based on the wrong equations can often be tuned to reproduce observed patterns perfectly, yet fail to generalize when conditions change. Similarly, a machine learning algorithm can perform impressively under cross-validation yet fail catastrophically when underlying regimes shift. This convergence of failure modes illustrates the pervasive challenge of getting the "right" answer for the wrong reasons (Beven 2006).

In addition to misspecification, there is another: semantic ambiguity. Even when both approaches are effectively "correct" on their own terms, researchers can arrive at robust but incompatible conclusions because they are effectively asking different questions of differently formalized objects. Disagreements often reflect not biology but rather the specific definitions of terms embedded in the math (as an example, see the sidebar titled Semantic Ambiguity in Action: What Is Interaction Strength?).

Importantly, these twin risks are not purely liabilities; viewed from the right angle, they can be diagnostic assets. Misspecification, for instance, can function as an informal null model: When a carefully parameterized model fails to reproduce an observed pattern, the failure itself can expose unknown biological processes—a signal that would have been invisible without the structural commitment. Similarly, semantic ambiguity, while dangerous when unrecognized, forces researchers to articulate their assumptions explicitly. The very act of discovering that two frameworks define "interaction strength" differently can catalyze a deeper understanding of what each framework is actually measuring. The goal, therefore, is not to eliminate these risks but to make them visible and productive.

The practical lesson is simple: before comparing claims across theories, we must ask what object each formalism has made measurable. Otherwise, different answers to different formal questions can be mistaken for a biological contradiction.

3. DISCIPLINING THE FORMALIZATION OF ECOLOGICAL THEORIES

The first principle is that you must not fool yourself—and you are the easiest person to fool.

—Richard Feynman (1974)

SEMANTIC AMBIGUITY IN ACTION: WHAT IS INTERACTION STRENGTH?

This example illustrates why merely comparing labels ("interaction strength is constant" versus "interaction strength varies") without understanding the underlying formalization can generate confusion that masquerades as scientific disagreement.

Suppose the true ecological dynamics follow a Lotka–Volterra system with fixed per capita interaction coefficients α_{ij}. A model-driven ecologist measures interaction strength as a static property of the species pair: α_{ij} is a constant that can, in principle, be estimated from controlled experiments (Novak et al. 2016). Now suppose a data-driven ecologist applies empirical dynamic modeling (specifically, S-maps) to time-series data generated by the same system. The estimated interactions will vary over time, because S-maps estimate the realized sensitivity of one species's growth rate to another's abundance at each time point. Because the aggregate impact of a species depends on current density, this effective interaction fluctuates with the system's state (Song & Saavedra 2021, Miki et al. 2025).

Both descriptions are mathematically correct, yet they paint opposite pictures: one of constancy, one of flux. The apparent contradiction is a semantic artifact: The two frameworks define "interaction strength" differently, and each is internally consistent.

A central challenge in ecological formalization is that we often have too much freedom in how we build models. To separate genuine biological insight from mathematical artifacts, models need stronger tests than they typically receive. In this section, I outline strategies to narrow that freedom in useful ways: anchoring models to shared benchmarks; filtering them through fundamental biophysical constraints; and using hybrid approaches that help discover, rather than assume, structure. The aim is not to promote a single preferred formalism but rather to make structural choices explicit, constrained, and easier to compare (**Table 1**).

3.1. From Idiosyncratic Checks to Shared Benchmarks

We must take validation seriously, not merely as a technical box to tick but as the primary means of defining what question a model is actually answering. We cannot expect full verification of ecological models in the sense of proving them "true" (Oreskes et al. 1994). Instead, validation

Table 1 Four ways to discipline ecological formalization

Strategy[a]	Core move	Guards against	Payoff	Section
Shared benchmarks	Compare theories on common data with common metrics	Idiosyncratic validation and one-off successes	Cumulative comparison and clearer failure modes	3.1
First-principles constraints	Filter models through existential conditions, logical consistency, and biological principles	Impossible or internally inconsistent structures	Smaller admissible model space	3.2
Hybrid discovery	Combine flexible learners with explicit process constraints	False choice between rigid mechanism and black-box fit	Flexible but interpretable models	3.3
Comparison and retirement	Compare failure modes and retire obsolete frameworks	Conceptual clutter and unchecked accumulation	A dynamic workspace rather than a theoretical museum	3.4

[a]Each strategy limits model freedom by making theories easier to compare, screen, or retire.

should be treated as a disciplined boundary-setting exercise: For which questions, under which conditions, and over which horizons does a given formalism provide reliable guidance?

Common task framework: a shared benchmark where different methods are tested on the same data with the same metrics

At present, new frameworks are frequently "validated" using only a handful of bespoke, hand-picked case studies. This reliance on bespoke validation makes it nearly impossible to discern whether a reported success reflects genuine robustness or merely the idiosyncrasies of the specific data employed (Augusiak et al. 2014, Qiao et al. 2015, Aldebert & Stouffer 2018, Terry & Armitage 2024).

To overcome this fragmentation, we must develop and adopt a common task framework: shared data sets combined with shared metrics (Donoho 2017). Other disciplines, such as computer vision, experienced rapid acceleration once diverse algorithms were routinely evaluated on common tasks (e.g., the ImageNet challenge; Deng et al. 2009). When different formalisms are forced to compete on the same playing field, it becomes easier to see which ideas generalize and which break down.

Network ecology provides a concrete example of how this can work. For instance, a line of research began with a provocative question: Can the structure of a species interaction network reveal whether the interactions are mutualistic or antagonistic (Michalska-Smith & Allesina 2019)? By formalizing this binary classification task and sharing standardized data sets, the community created a common playing field. Successive teams then competed to improve classification accuracy (Song & Saavedra 2020, Brimacombe et al. 2022, Pichon et al. 2024, Biton et al. 2025), and the progression exposed which topological features were robust discriminators and which were artifacts of sampling bias. This lineage of competitive refinement, sparked by a single, concrete benchmark, illustrates how a common task framework converts isolated proof-of-concept studies into cumulative, self-correcting science.

This is not an isolated case. Ecology is beginning to build analogous infrastructures in other domains. The Ecological Forecasting Initiative's NEON Forecasting Challenge, for example, allows diverse modeling approaches to be compared against standardized targets (Dietze et al. 2018, Thomas et al. 2023). Together, these efforts show that benchmark-driven validation is an emerging strategy for making theoretical comparison cumulative across ecology.

Crucially, such benchmarks are predicated on massive infrastructural investments. The NEON Forecasting Challenge relies on the institutional stability of a long-term national observatory, a project requiring decades of vision and funding (Thomas et al. 2023). Similarly, the network ecology benchmarking effort was possible only because of decade-long data-aggregation efforts (e.g., Fortuna et al. 2014, Vissault et al. 2019, Fricke & Svenning 2020). These repositories effectively constructed the ground truth needed to train and test the competing theories. To extend this rigor across ecology, we must prioritize the creation of analogous benchmarks in other subdisciplines, recognizing that shared data are the prerequisite for shared understanding.

Benchmarks need not be exclusively empirical; standardized in silico testbeds are equally important. Currently, the validation of new inference methods typically relies on ad hoc simulations generated by the authors themselves (Lotterhos et al. 2022). This is insufficient. To rigorously vet theoretical tools, we need curated libraries of synthetic "model worlds" spanning diverse parameter regimes, noise structures, and observation schemes. Because the generative truth in these libraries is known perfectly, they allow researchers to systematically map the failure modes of new methods (Runge et al. 2019, Ferdous et al. 2025), distinguishing algorithmic artifacts from genuine discovery.

Complementing these empirical and synthetic benchmarks, a parallel imperative is to leverage systems where observational inference can be checked against independent knowledge of the truth. In economics and political science, the influential LaLonde (1986) study played this role by asking whether nonexperimental methods could reproduce the results of randomized control trials (Imbens & Xu 2025). Ecological analogues are now emerging. For example, ecologists have

simultaneously analyzed regional co-occurrence data alongside independent evidence of interactions derived from serology or detailed natural history (Barner et al. 2018, Freilich et al. 2018, Brazeau & Schamp 2019, Thurman et al. 2019). These dual-data systems have been decisive in demonstrating that co-occurrence is often a misleading proxy for ecological interaction (Blanchet et al. 2020, Goberna & Verdú 2022). Ecology's rich legacy of manipulative experiments and natural history constitutes a reservoir of ground truth that many other scientific disciplines would envy—an underutilized asset we are uniquely positioned to mobilize for validation.

Label invariance: the logical requirement that a model's predictions should not change if identical organisms are simply renamed or arbitrarily regrouped

Metabolic theory of ecology: a theory that links ecological rates (e.g., metabolism, growth rate) to body size and temperature using scaling laws

3.2. Filtering Admissible Models with First Principles

We must harness fundamental constraints—independent of any particular data set—to discipline the search for admissible models. A model-driven analysis can select from a vast dictionary of functional responses, interaction terms, and noise structures; a data-driven analysis can vary architectures, embedding dimensions, and hyperparameters (the structural settings of the algorithm). Fundamental constraints provide a rigorous filter: They rule out large classes of models before we assess empirical performance, serving as the first line of defense against pathological behavior.

The first layer of constraints consists of existential conditions: the basic facts of life for populations. First, ecological state variables such as abundance or biomass cannot be negative. This simple condition, known as feasibility, may seem trivial but has nontrivial consequences for coexistence theory (Roberts 1974, Saavedra 2026). Second, populations cannot grow without bound: Reproduction and survival are ultimately capped by finite resources and physiological limits. Recognizing this constraint has been crucial for refining models for mutualistic interactions (May 1976, Bascompte et al. 2006, Holland et al. 2006, Hale & Valdovinos 2021). Finally, new individuals arise only from existing organisms. In the absence of immigration or speciation, models of population change are necessarily framed in terms of per capita growth rates. These constraints are foundational because they dictate the admissible forms of ecological equations.

The second layer imposes logical consistency. Certain transformations of a system's description should not alter its ecological conclusions. A key criterion is label invariance: If members of a group of individuals are functionally indistinguishable in their traits and interactions, the model's output must remain identical whether we label them as one species or split them into two arbitrary groups. This requirement provides a sharp consistency check that many prominent models fail (Ansmann & Bollenbach 2021, Moisset de Espanes et al. 2021, Gibbs et al. 2025). Similarly, spatial models must satisfy a perfect mixing condition: If dispersal between two patches becomes instantaneous, the system must be mathematically indistinguishable from a single, aggregate population. Models that do not recover this nonspatial limit are structurally flawed (Arditi et al. 2016). Other studies have proposed analogous consistency checks to further constrain the set of admissible models (Wontner & Spencer 2025).

The third layer arises from physical and biological principles. I distinguish two categories of such constraints. One category consists of those derived from conservation laws, which impose hard boundaries on system fluxes; energy and mass balance dictate strict limits on transfer efficiencies (Loreau 2010, Schmitz & Leroux 2020), while ecological stoichiometry constrains consumer dynamics on the basis of elemental ratios (Sterner & Elser 2002, Sinsabaugh & Follstad Shah 2012). The other category comprises constraints derived from scaling laws, which reduce the dimensionality of parameter space by linking rates to measurable properties. Rather than treating model parameters as free variables, these laws enforce covariance. For example, the metabolic theory of ecology scales metabolic and demographic rates with body size and temperature (Brown et al. 2004, Munch et al. 2023b, Vasseur et al. 2025). Similarly, functional trait frameworks scale interaction strengths with phenotypic matching and physiological trade-offs

(Litchman & Klausmeier 2008, Kunstler et al. 2016, Wickman et al. 2024). In both cases, general biological rules replace arbitrary parameter fitting.

Symbolic regression: an algorithm that searches the space of mathematical expressions to find equations that best fit the data, discovering both structure and parameters simultaneously

The goal here is not to force all models into a narrow mold (Rudin et al. 2024) but rather to ensure that this freedom is exercised within a space that is at least qualitatively compatible with what we know independently of any particular data set. Fundamental constraints, understood in this broad sense, do not eliminate misspecification. Instead, they serve as powerful priors, regularizers, or diagnostic baselines that guide models away from biologically impossible regimes.

3.3. Bridging Imposing and Discovering Models

Another fruitful path forward is to dissolve the rigid boundary between discovering structure and imposing it. Rather than treating process-based models and machine learning as competing camps, a growing body of research integrates them into hybrid frameworks. In this view, flexible algorithms search the space of possible model structures, while physical or biological principles serve as guardrails for otherwise black-box learners. Ecology has begun to move in this direction, yet the space of possibilities remains vastly underexplored.

The best-known approach in ecology is symbolic regression (Martin et al. 2018, Chen et al. 2019). Here, algorithms search the space of mathematical expressions to find the equations themselves, selecting both structure and parameters to best match the data. While this strategy has proven highly effective for model discovery in physics (Udrescu & Tegmark 2020, Shen et al. 2023), its application in ecology has been constrained by the stochasticity and sparsity of biological data. However, recent breakthroughs are overcoming these limits, for example, by adapting transformer-based methods (the same neural network architectures underlying large language models) to robustly infer differential equations from noisy, short time series (d'Ascoli et al. 2024).

A complementary approach discovers structure by identifying invariants—mathematical relationships that must hold true regardless of parameter values—rather than by estimating the parameters themselves. By adapting results from queueing theory (Hilfinger et al. 2016), recent research has derived such constraints for ecological dynamics (Song & Levine 2025). Because these relationships are structural necessities rather than fitted trends, empirical violations can invalidate the hypothesized model form even when parameters are poorly known and other species in the community are unobserved.

A third, emerging approach is scientific machine learning, which fuses neural networks with differential equations. Methods such as physics-informed neural networks and universal differential equations can embed known biological laws directly into the learning process (Rackauckas et al. 2020, Karniadakis et al. 2021). For example, logical constraints and biophysics constraints can be encoded in the loss function (the target the algorithm tries to minimize) or in the network architecture, ensuring that predictions satisfy both the data and the governing biology (Bonnaffé et al. 2021).

Across these approaches, discovery is never fully automated. The common theme is that the computational learner and the human modeler are inseparable: Process-based equations provide a scaffold within which flexible algorithms interpolate or adjust unknown terms, balancing mechanistic fidelity with empirical fit.

3.4. Life Cycle of Ecological Theory: Comparison and Retirement

Ecological theory currently suffers from a fundamental imbalance: The incentives to create new frameworks far outweigh the incentives to systematically evaluate existing ones. This asymmetry produces so-called conceptual clutter, a state where active, robust tools are indistinguishable

from those that have been superseded. Resolving this problem requires that we treat comparative research not as a secondary exercise but as a primary mechanism of theoretical hygiene. We should elevate studies that benchmark models against shared data sets and normalize the explicit reporting of failure modes: clearly delimiting where a model breaks down so that future researchers do not mistake a limitation for a puzzle (Fanelli 2012, Houlahan et al. 2017).

However, rigorous comparison is only useful if we act on its verdicts. When accumulated evidence suggests that a framework is a dead end, we must be willing to retire it. Currently, the field lacks a clear exit strategy for obsolete ideas; we need to create publication space for assessments that explicitly argue for the abandonment of modeling traditions when they no longer serve their purpose (Mallet 2012, Fox 2013, Abrams 2015). Crucially, retirement does not mean erasing a model from history. Rather, it means reclassifying it: moving it from the toolkit of active inquiry to the library of historical reference or pedagogical baselines.

This discipline of "letting go" is the necessary counterpart to our tradition of "welcoming in." Ecology has thrived by maintaining an open border to tools from physics, mathematics, and computer science (Marquet et al. 2014). We should continue to welcome these innovations. But to do so without collapsing under the weight of accumulating complexity, we must treat the theoretical toolkit as a dynamic workspace, not a museum. A tool is only as valuable as the work it enables; when better tools arrive, the old ones should be gratefully, but firmly, set aside.

4. FUNCTIONS OF ECOLOGICAL THEORY: WHY ECOLOGISTS BUILD MODELS

> Theories are nets: only he who casts will catch.
>
> —Novalis [1837 (1798), p. 211]

Formalization describes the anatomy of a model, but it does not capture its intent. Equally critical is the dimension of function: the specific purpose a model is designed to serve. Because two mathematically identical structures can be deployed to answer radically different questions, confusion inevitably arises when these underlying purposes remain unarticulated.

To isolate the role of function, consider a thought experiment. Imagine a world of empirical omniscience, a scenario where all technical barriers to observation have vanished. In this world, we can measure every relevant state variable, track every individual organism, resolve every trophic interaction, and manipulate any biologically possible process. Would theory become obsolete?

It would not (Coveney et al. 2016). We would still require tools to compress complexity into usable summaries, to assign precise meaning to our ecological vocabulary, and to explore counterfactual regimes beyond the systems we happen to observe. Perfect data would remove the practical obstacles to information, but they would not, by themselves, tell us how to organize that information or which questions to ask. Theory is what turns a glut of facts into structured knowledge.

Seen from this perspective, ecological theory performs at least three distinct, indispensable functions (Table 2). First, it constructs predictive heuristics (prediction)—simple conditions or compressed metrics that summarize complex dynamics to guide expectation. Second, it provides definitional frameworks (definition)—accounting systems that standardize ecological language and partition mechanisms. Third, it enables theoretical experiments (experiment)—model worlds that allow us to probe the logical consequences of assumptions and map the boundaries of the possible. Each of these functions remains essential even in a data-rich world, yet each is prone to characteristic forms of misinterpretation that fragment our field.

Table 2 Three functions of ecological theory

Function[a]	Primary goal	Characteristic error	Pathway to synthesis	Section
Predictive heuristic	Compress complex dynamics into actionable summaries	Semantic overload: same label, different mathDomain mismatch: heuristic applied outside its derivation regime.	Systematically extend heuristics to new contexts; publish explicit domains of validity	4.1
Definitional framework	Standardize vocabulary and partition mechanisms	Reification: treating accounting terms as physical entitiesPolysemy: competing definitions under the same label	Build explicit translation rules between frameworks; treat polysemy as a diagnostic asset	4.2
Theoretical experiment	Explore "what if" scenarios in model worlds	Misplaced dismissal: rejecting models for lacking realismOvergeneralization: treating narrow results as universal laws	Situate experiments on explicit organizational axes (scale, process, dynamical regime)	4.3

[a]Each function serves a distinct purpose, is prone to a characteristic form of misinterpretation, and benefits from a specific pathway to synthesis. Recognizing which function a given framework serves is the first step toward disciplined synthesis.

4.1. Predictive Heuristics: Compressed Foresight

A central ambition of ecological theory is to distill the sprawling complexity of nature into tractable foresight. By a predictive heuristic, I mean a relatively low-dimensional summary—often a scalar condition or inequality—that acts as a proxy for the key behavior or outcome of a complex system. Such heuristics allow managers and empiricists to turn high-dimensional, often noisy, information into actionable judgments: Will this invasive species establish? Is this community robust to disturbance?

Heuristic: a simplified rule of thumb or mathematical shortcut used to make tractable predictions

Modern coexistence theory: studies coexistence using invasion growth rates

Invasion growth rate: the average per capita growth of a species when rare in a resident community

Structural stability: studies coexistence by asking over how wide a range of conditions all species can persist

Coexistence theory offers several clear examples. Modern coexistence theory, for instance, recasts the challenging problem of multispecies coexistence into the calculation of invasion growth rates, replacing a system of differential equations with a single check for positivity (Grainger et al. 2019). Structural stability approaches perform an alternative compression, summarizing a community's tolerance to environmental change via the volume of parameter space compatible with positive abundances (Saavedra et al. 2017, Song 2020).

This logic of predictive compression can be appreciated in the classic test of niche versus neutral explanations in annual plant communities (Levine & HilleRisLambers 2009). A simple predictive heuristic would treat similarity as the relevant shortcut: Demographically similar species should compete more strongly and therefore be less likely to coexist. Levine and HilleRisLambers made this intuition operational by asking whether species can increase when rare and whether conspecific limitation exceeded heterospecific limitation. In doing so, they compressed a high-dimensional community problem—many species, many interactions, and many environmental contingencies—into a smaller set of demographic quantities tied to invasion growth.

This empirical example also shows why such heuristics require care. Similarity is not itself a prediction. It is useful only when it tracks the demographic processes that determine invasion growth rates. When trait, phylogenetic, or resource-use similarity fails to map cleanly onto stabilizing niche differences and fitness differences, the heuristic can mislead even when the underlying coexistence theory is sound (HilleRisLambers et al. 2012, Barabás et al. 2018, Adler et al. 2026).

This is the power and danger of heuristics. They are powerful because they compress. They identify the specific combination of variables that matters for a particular question and strip away the rest. Yet, this very efficiency is also the primary architect of confusion.

The first challenge is semantic overload. We frequently assign identical verbal labels to mathematically distinct quantities. The most widely recognized example is "stability." This term may refer variously to recovery speed (asymptotic stability), robustness to changing environment (structural stability), or the likelihood of avoiding extinction (stochastic persistence). This semantic overload is perhaps the most revisited problem in ecological theory, prompting a major synthesis with ritualistic regularity roughly once a decade (Lewontin 1969, Orians 1975, Pimm 1984, Grimm & Wissel 1997, Ives & Carpenter 2007, Donohue et al. 2016, Chen et al. 2024).

A parallel, less scrutinized but no less important example is the heuristic of limiting similarity. For decades, this principle has served as a predictive gatekeeper: If species are too similar, exclusion is predicted. Yet, the metric of similarity suffers from profound semantic drift. It is applied interchangeably to static proxies, such as phenotypic distance (Do they look alike?) and resource overlap (Do they eat the same things?) (Abrams 1983), versus dynamical definitions derived from modern coexistence theory (Chesson 2000) or sensitivity theory (Meszéna et al. 2006). This ambiguity has fueled decades of debate regarding the limits to limiting similarity, with the concept oscillating between dismissal as a mathematical artifact (Abrams 1983) and defense as a fundamental rule of nature (Pásztor et al. 2016).

However, even when concepts are unambiguous, another risk remains: domain mismatch. Because heuristics are simplifying summaries, they are valid only under specific regimes. These constraints are easily forgotten once a metric becomes the field's standard. For example, local asymptotic stability is designed to describe a system's recovery from infinitesimal perturbations near an equilibrium. When applied to questions involving small but finite perturbations, this heuristic is, strictly speaking, outside its remit. Such questions are better served by other concepts, such as global stability (Lewontin 1969), permanence (Hofbauer & Schreiber 2022), or basin stability (Menck et al. 2013). When a heuristic is stretched beyond the limits of its derivation, its apparent predictions can be misleading. These considerations point to an actionable imperative: Researchers who develop or deploy predictive heuristics should explicitly publish the domain of validity: the parameter regimes, system sizes, and dynamical assumptions under which the heuristic has been tested and found reliable. Journal editors and reviewers, for their part, should require such boundary statements as a standard component of any paper proposing a new predictive metric. Without this discipline, the field risks accumulating an ever-larger toolkit of powerful but unlabeled instruments.

Limiting similarity: the idea that there is an upper limit to how similar competing species can be in resource use before coexistence breaks down

Sensitivity theory: studies coexistence via how equilibrium densities change under small shifts in traits or interactions

Permanence: ensures that all species populations will remain above zero indefinitely, regardless of their initial densities

Basin stability: how large a perturbation can be that still lead the system back to the same equilibrium or attractor

4.2. Definitional Frameworks: Theory as Accounting System

Many of the quantities we talk about in ecology do not correspond to pregiven objects "out there" in nature. A primary function of theory is to provide the grammar of ecology: to define concepts and partition processes in ways that organize our observations and reasoning. Data can tell us what happened, but they cannot, by themselves, determine how to assign those events to specific mechanisms or which partitions of variation are most informative.

Some frameworks are primarily typological. The classification of interaction types into competition, predation, mutualism, and commensalism supplies a standardized vocabulary for qualitative effects (Mathis & Bronstein 2020). The definition of distinct interaction motifs, such as apparent competition and intraguild predation, supplies a shared grammar for labeling the elemental building blocks of food webs (Dormann et al. 2017, Holt & Bonsall 2017). In these cases, theory offers a necessary convention: It allows us to agree on what we are looking at before we attempt to explain it.

Other frameworks are explicitly partitioning. These approaches decompose a net observable outcome into additive or multiplicative terms associated with distinct processes. In biodiversity–ecosystem functioning research, the Loreau–Hector partition separates the net biodiversity effect into complementarity and selection components (Loreau & Hector 2001, Tilman et al. 2014). In modern coexistence theory, the invasion growth rate is decomposed into stabilizing mechanisms (niche differences) and equalizing mechanisms (fitness differences) (Chesson 2000, Barabás et al. 2018). Crucially, these constructions do not uncover distinct physical entities that exist independently of our equations; rather, they propose specific ways of partitioning portions of an observed response into conceptual bins.

Biodiversity–ecosystem functioning: how species richness and composition affect ecosystem processes like productivity

Loreau–Hector partition: partitions the net biodiversity effect into selection and complementarity components

Niche difference: the extent to which species limit their own growth more than they limit that of others

Fitness differences: persistent performance advantages that make one species a better competitor than another

Because definitional frameworks are tautologies based on mathematical identities, they occupy a distinctive position in ecological theory. They are not empirical hypotheses that can be falsified by data; rather, they are accounting systems. One cannot disprove the Loreau–Hector partition any more than one can disprove the rule that income equals revenue minus expenses. Thus, the relevant criterion is not "Is it true?" but rather "Is it useful?" Does a given decomposition align with our biological intuition and highlight informative contrasts?

Darwin's naturalization conundrum offers a paradigmatic illustration of this utility. Verbal intuition yields a paradox: Closely related species are expected to compete more strongly (hindering invasion via limiting similarity), yet they simultaneously share the adaptations required to survive the local environment (facilitating invasion via environmental filtering) (Cadotte et al. 2018). Modern coexistence theory tackles this tension by providing a quantitative accounting ledger (HilleRisLambers et al. 2012). It maps the competitive liability of similarity onto niche differences and the environmental benefit of similarity onto fitness differences. This formalization transforms a qualitative ambiguity into two quantitative categories.

However, the very abstraction that makes this type of accounting powerful also invites two characteristic forms of conceptual error. The first is reification: treating terms in a definitional framework as if they were concrete, measurable entities in nature. For instance, niche differences are frequently discussed as if they were tangible biological features like root depth or beak size. In reality, while such traits may cause niche differences, the metric itself is an aggregate statistical summary of how density dependence restricts population growth (D'Andrea & Ostling 2016). This confusion is not merely user error; borrowing everyday terms makes it easy to slide between biological intuition and formal quantity.

The second form of conceptual error is polysemy: the proliferation of competing, nonequivalent definitions under the same label. There are now at least seven alternative definitions of "niche difference" and "fitness difference," all presented under the banner of modern coexistence theory (Spaak & De Laender 2020). These definitions can assign not only different numerical values but also different qualitative interpretations to the exact same dynamics (Song et al. 2019, Spaak et al. 2023a). Without explicit acknowledgment of which definition is being deployed, empirical comparisons and meta-analyses risk collapsing distinct concepts into a meaningless aggregation.

4.3. Theoretical Experiments: Model Worlds and Possible Ecologies

Aside from prediction and definition, a third function of theory is to serve as a laboratory for model worlds. While we typically associate experiments with field manipulations or laboratory benches, the fundamental logic of experimentation is controlled comparison: systematically varying one factor while holding others fixed to isolate a causal effect. Theoretical experiments extend this logic to models, allowing us to ask "what if" questions that would be impractical, unethical, or physically impossible to execute in nature.

Even in an idealized world of perfect empirical access, theoretical experimentation would remain indispensable. In real ecosystems, processes are often inextricably entangled: Species with similar traits tend to be phylogenetically related, and environmental conditions fluctuate in messy, unpredictable ways. Theory allows us to decouple these factors. We can construct model worlds where traits evolve independently of phylogeny, where species are ecologically identical, or where environmental variability follows a controlled pattern. These are investigations into possible worlds that isolate mechanisms in ways that nature simply does not permit.

Random matrix: a mathematical object where interaction strengths between species are drawn at random from a probability distribution

An archetype of this function is Robert May's (1974) seminal analysis of diversity and stability. Empirical observation suggested a positive correlation between diversity and stability, but observation alone could not determine whether diversity caused stability or whether both were products of assembly and succession processes. By turning to random matrix theory, May designed a theoretical experiment: He constructed a null world of random interactions, devoid of any biologically meaningful structure. The finding that diversity begets instability in this null world was not a contradiction of nature but a proof by contradiction: It demonstrated that the observed stability of real ecosystems must stem not from their diversity per se but instead from the specific, nonrandom biological structure of their interactions.

As empirical tools advance, the boundary between theoretical and empirical experimentation is dissolving. Questions once reserved for abstract mathematics—such as whether population fluctuations are endogenous or environmentally driven (Myers & Cory 2013), or the conditions for chaos (Munch et al. 2022)—are now being probed in microbial microcosms and synthetic communities where interaction networks are experimentally programmable (Gore & You 2022). Yet even these sophisticated experiments cover only a tiny fraction of the relevant parameter space. Model worlds remain essential for mapping the vast terra incognita that lies beyond the reach of the pipette or the hand of the field ecologist.

At the same time, theoretical experiments are prone to characteristic forms of misunderstanding that contribute to fragmentation. A persistent one is misplaced dismissal: rejecting a theoretical experiment because its assumptions do not mirror the full complexity of a specific system.

Critiques of abstract models have persisted, ranging from accusations of "physics envy" (Egler 1986) to debates over the utility of null models (Harvey et al. 1983, Roughgarden 1983) to recent debates over idealization and model realism in ecology (Justus 2021, Morrow 2024). Such dismissal, however, misunderstands the function of an experiment. The artificiality of the model is not a flaw but a design feature: It allows us to isolate a specific mechanism from the noise of reality (Levins 1966, Odenbaugh 2005). While this rationale is widely accepted in principle, the reflex to penalize models for lacking realism remains a persistent barrier in peer review.

Another, almost opposite problem is overgeneralization: treating a result derived from a specific logical test as a universal law. May's complexity metric, for example, is a precise mathematical statement about the properties of random matrices, yet it is frequently invoked as if it were a direct measure of the complexity of real, nonrandom communities (Jacquet et al. 2016). Here, the danger is that the narrow domain of the theoretical experiment quietly disappears from view; when the assumption of randomness is violated, applying this metric constitutes a transgression of domain, rendering the resulting comparisons mathematically problematic.

4.4. When Functions Collide: The Perils of Multifunctionality

The three functions of theory—prediction, definition, and experiment—can seem so different that it is tempting to assume no one would ever confuse them. In practice, however, such confusion is common. A primary reason is that ecology's most successful theories are often multifunctional. Modern coexistence theory, for instance, operates simultaneously across all three functions: It provides predictive heuristics (invasion growth rates) to forecast outcomes, it offers a definitional

framework (partitioning growth rates into niche and fitness differences) to organize concepts, and it serves as a platform for theoretical experiments (e.g., removing environmental fluctuations to isolate storage effects).

Intermediate disturbance hypothesis: the hypothesis that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent

Unified neutral theory of biodiversity (i.e., neutral theory): assumes individuals of different species are ecologically equivalent and explores how drift and dispersal alone can shape diversity patterns

Niche–neutrality continuum: the view that real communities lie between two extremes: purely niche structured and purely neutral, with both processes contributing

When the intended function of a model is not explicitly bounded, researchers inadvertently slide between modes. A definitional partition is critiqued as if it were a falsifiable hypothesis, a theoretical experiment is rejected because it lacks the precision of a forecast, or a predictive heuristic is mistaken for a fundamental law.

These are not hypothetical confusions. The same diagnostic lens clarifies several familiar debates in community ecology. In biodiversity–ecosystem functioning research, the Loreau–Hector partition was designed as a definitional accounting device: It decomposes the net biodiversity effect into selection and complementarity components. Difficulties arise when those accounting terms are treated as separable physical mechanisms waiting to be isolated in nature; debate can then drift away from the appropriate question (Which biological contrasts does the partition make visible?) toward the less appropriate question of whether the partition has discovered two independent causal substances (Loreau & Hector 2001, 2019; Pillai & Gouhier 2019). May's diversity–stability result illustrates a different functional mismatch: It was a theoretical experiment about random matrices near equilibrium, yet it has often been rejected as a poor empirical forecast for real food webs, or invoked too broadly as a general law about ecological complexity (May 1974, Jacquet et al. 2016). The intermediate disturbance hypothesis represents a third variant, in which a verbal predictive heuristic hardened into presumed law: A context-dependent idea that disturbance can maintain diversity by preventing competitive dominance became widely evaluated as though it predicted a universal hump-shaped relationship between disturbance and species richness (Fox 2013). These examples differ in content, but they share the same diagnostic structure (Blüthgen & Staab 2024): Debate became unproductive when researchers evaluated a definitional partition, a theoretical experiment, or a predictive heuristic using the wrong standard of success.

The unified neutral theory of biodiversity (i.e., neutral theory) represents an especially revealing case (Hubbell 2001), as it can be interpreted as a predictive theory, a statistical null, or a theoretical experiment. In short, neutral theory poses a radical counterfactual: What if individuals of different species are demographically equivalent? The subsequent decade of debate hinged less on the internal mathematics than on the model's intended function. Was it a literal predictive theory competing with niche mechanisms? If so, extensive testing suggested that it failed, as species are demonstrably not equivalent (McGill 2003, Wootton 2005, Levine & HilleRisLambers 2009). Alternatively, was it a statistical null model (Alonso et al. 2006, Rosindell et al. 2012)? Critics argued that because neutral theory is a mechanistic model with fitted parameters, it cannot serve as a statistical randomization test (Gotelli & McGill 2006, Clark 2012). Although the field has since largely reconciled these views by positioning neutrality as an anchor point on a niche–neutrality continuum (Adler et al. 2007; but see Song et al. 2019, Kessler & Shnerb 2025)—effectively treating it as a theoretical experiment—this resolution was hard won, succeeding only because the model's central provocation was too important to ignore.

Explicitly stating the intended function—or functions—of a theory is a practical necessity, not a semantic luxury. Without this clarity, less prominent frameworks rarely survive the friction of cross-disciplinary debate. They are frequently discarded prematurely for failing predictive tests they were never designed to pass, or they linger in conceptual ambiguity indefinitely.

5. SYNTHESIZING THE FUNCTIONS OF ECOLOGICAL THEORIES

> [I]n almost every one of the leading controversies... both sides were in the right in what they affirmed, though wrong in what they denied.
>
> —John Stuart Mill (1840, p. 261)

The preceding sections distinguish what ecological theories are for, as well as how each contributes to conceptual fragmentation. I now turn to strategies for achieving synthesis within each of these domains. The aim of this section is to describe concrete routes for unifying fragmented traditions and for integrating existing attempts at synthesis.

Contemporary niche theory: studies coexistence via how species deplete and are limited by shared resources and other regulating factors

Priority effects: when the order or timing of species arrival changes which species persist or the functioning of the community

5.1. Expanding the Generality of Predictive Heuristics

Predictive heuristics are inherently approximate; they trade rigorous detail for useful compression. Consequently, the pathway to synthesis is not to perfect their precision but rather to systematically expand their applicability. We must determine how far these summaries can be stretched across new contexts before they lose their utility. A growing body of research in coexistence theory is now undertaking this extension, pushing the boundaries of established metrics along three distinct axes.

The first line extends heuristics beyond purely competitive interactions. The two dominant frameworks, contemporary niche theory and modern coexistence theory, were originally developed for negative interactions mediated by shared limiting resources. Recent studies demonstrate that their core constructions can be carried over, with suitable modification, to encompass predation and mutualism (Koffel et al. 2021, Spaak et al. 2021b, Valdovinos & Marsland 2021). This unification allows distinct interaction types to be compared using a shared currency.

The second line broadens the outcomes these heuristics are used to predict. Classic invasion criteria were tuned to a binary result: stable coexistence or competitive exclusion. More recent studies reinterpret these metrics not as simple yes/no tests but as predictors of a richer catalog of dynamical scenarios. These include priority effects (Fukami 2015, Ke & Letten 2018, Song et al. 2021) as well as community disassembly (species loss) (Angulo et al. 2021, Song 2025, Brennan & Schreiber 2026).

The third line confronts the complexity and realism of the communities in question. While operational uses of coexistence theory have historically focused on pairs of competitors, recent research has successfully extended these heuristics to multispecies communities at a single trophic level (Spaak et al. 2021a, Ranjan et al. 2024) as well as across multitrophic levels (Guzman et al. 2019, Song & Spaak 2024). Parallel efforts are bridging the gap between idealized, continuous-density models and the reality of finite, stochastic populations (Schreiber et al. 2023), while also linking invasion criteria to rigorous mathematical foundations (Hofbauer & Schreiber 2022, Spaak & Schreiber 2023, Schreiber et al. 2026).

Taken together, these efforts in coexistence theory illustrate a general lesson for synthesis. Predictive metrics such as invasion growth rates or feasibility domains (Cenci & Saavedra 2018, Luo et al. 2022, Lechón-Alonso et al. 2026) need not be confined to narrow domains. By systematically testing how far they can be extended, we transform them into reusable summary currencies. Crucially, this process also exposes their failure modes. Not every extension will succeed, and those failures are themselves informative: They highlight which combinations of processes act as truly general operators in our ecological models and which are strictly context dependent. In this way, predictive heuristics evolve from specific solutions into general tools for synthesis.

5.2. Linking Definitional Frameworks to Translate Between Currencies

Because definitional frameworks function as accounting systems rather than falsifiable hypotheses, synthesis requires a different standard of success. The relevant question is not which definition is "true," but instead how distinct accounting schemes map onto one another. This is possible because the vast majority of ecological partitions share a common mathematical architecture, typically rooted in Lotka–Volterra or consumer–resource dynamics. This shared mathematical architecture acts as a kind of Rosetta Stone: It allows us to write distinct definitions in the

same symbols and, in principle, derive explicit translation rules between frameworks that would otherwise seem conceptually disjoint.

This synthesis is already underway. For coexistence theory, explicit mappings now connect contemporary niche theory, modern coexistence theory (Letten et al. 2017, Sakarchi & Germain 2025), and the structural stability approach (Song et al. 2020). Analogous bridges are being built across neighboring subfields by reexpressing diverse frameworks on common dynamical backbones. Successful examples include selection-complementarity partitions in biodiversity–ecosystem functioning (Wang et al. 2021, Wan et al. 2025), process-based decompositions in metacommunity theory (Shoemaker & Melbourne 2016), scaling relationships in the metabolic theory of ecology (O'Connor et al. 2025, Saavedra et al. 2025, Davis et al. 2026), and transmission partitions in disease ecology (Sieben et al. 2022, Park et al. 2024). In effect, many traditions are keeping the same books in different currencies. Translation, therefore, does more than tidy up vocabulary; it allows theoretical insights, and even parameter estimates, to be exported from one domain to another with a quantified change of basis.

At the same time, translation has genuine limits. The most obvious arise from polysemy: multiple, nonequivalent definitions circulating under a shared label such as "niche difference." It is tempting to imagine that this confusion could be resolved by agreeing on a single canonical definition. However, a deeper limitation lies in the irreducibility of the underlying dynamics. The core difficulty is not partitioning per se but rather the attempt to impose linear, additive decompositions on systems that are fundamentally nonlinear. In such systems there is, in general, no unique way to assign a fixed share of a response to any given "mechanism": Any additive split depends on the choice of reference state, the order in which effects are attributed, or the path along which the system is perturbed.

This nonuniqueness due to irreducibility is well-known outside ecology, for example, in additive decompositions of wage gaps in labor economics (Fortin et al. 2011) and in feature-importance methods in machine learning (Verdinelli & Wasserman 2024). The same issue arises in ecological partitions. In modern coexistence theory, stabilizing (niche) and equalizing (fitness) components are mathematically entangled: Small parameter changes typically alter both simultaneously, and the same perturbation can even reverse the apparent ranking of which mechanism is "doing the work" (Barabás et al. 2018, Song et al. 2019, Spaak et al. 2023b). In biodiversity–ecosystem functioning, debate around the Loreau–Hector selection–complementarity partition has likewise shown that the relative size of the two terms is sensitive to scaling and baseline choices rather than reflecting two cleanly separable processes (Loreau & Hector 2019, Pillai & Gouhier 2019). Polysemy is, in large part, a mathematical consequence of this irreducible nonuniqueness.

Given this irreducibility, the goal cannot be to eliminate polysemy altogether but instead to manage it productively. Rather than forcing premature consensus, we can treat coexisting definitions as a diagnostic asset. Comparing alternative partitions plays a role analogous to sensitivity analysis: When different definitions agree, we gain confidence that a reported pattern is not an artifact of a particular bookkeeping scheme; when they diverge, the discrepancies pinpoint exactly which modeling choices—such as how nonlinearity is averaged, or which reference is chosen—are driving different narratives.

Recognizing nonuniqueness does not diminish the importance of definitional frameworks—quite the opposite. When treated explicitly as coordinate systems rather than as unique biological realities, they become powerful tools. Linking frameworks where possible, and documenting precisely where they resist reconciliation, helps us distinguish properties that are robust to changes of definition from those that are artifacts of particular mathematical choices. To make this point concrete, consider how translation works between contemporary niche theory and modern coexistence theory. Both frameworks describe coexistence in settings that can be reduced to a shared

Lotka–Volterra backbone. Contemporary niche theory partitions this system into resource-supply points and zero-net-growth isoclines, asking whether species deplete different resources; modern coexistence theory partitions the same system into niche differences (how much species limit themselves versus one another) and fitness differences (who would win in the absence of niche differentiation). The explicit mappings between these two partitions (Letten et al. 2017) allow a result expressed in one currency (say, a measured resource-supply ratio) to be reexpressed in the other (as a quantified niche difference).

Zero-net-growth isocline: the set of environmental conditions (e.g., resource availability) under which a species' population growth rate is exactly zero

For empiricists navigating this landscape, a practical guideline emerges: When encountering a metric such as niche difference or complementarity, always check which definition is being used and under which reference conditions it was computed, and report them explicitly in publications. When comparing results across studies, first verify that the definitions are commensurable; if they are not, consult the available translation rules or, at a minimum, flag the discrepancy. Treating polysemy as a diagnostic tool—rather than an obstacle—empowers researchers to extract signal from apparent noise.

In summary, definitional work contributes to synthesis not by delivering a single canonical partition but by charting the space of admissible partitions. In doing so, it clarifies how our conceptual bookkeeping shapes the ecological stories we tell.

5.3. Organizational Axes of Theoretical Experiments

The opposing risks of dismissing abstract models and overgeneralizing stylized results are best mitigated by situating theoretical experiments along a defined set of organizing axes. In practice, every theoretical experiment varies specific aspects of ecological complexity while holding others fixed. By explicitly structuring these choices within a landscape of assumption and complexity, we transform a scattered collection of idiosyncratic models into a navigable map of possible worlds.

The most influential coordinate system focuses on scale. Ecological phenomena are naturally structured along spatial, temporal, and organizational scales, and much confusion stems from mixing mechanisms or measurements across these without care (Levin 1992). Recent research has operationalized this perspective, such as in biodiversity–ecosystem functioning (Gonzalez et al. 2020) and interaction structure across levels of biological organization (Guimaraes 2020). Here, synthesis is achieved by explicitly stating which scales are held fixed and which are allowed to vary, transforming seemingly contradictory results into consistent scalable relationships.

Another major coordinate system organizes theoretical experiments by fundamental processes: selection, drift, dispersal, and speciation (Vellend 2016). In this view, models are compared not according to their specific equations but in terms of their relative emphasis on these four forces. Such comparison allows diverse theoretical traditions to be plotted as specific locations within a shared process space. For example, this perspective has been used to synthesize metacommunity theory by demonstrating that the classic four archetypes (e.g., patch dynamics, species sorting) are not distinct theories but rather special cases—or specific corners—within this broader process-based continuum (Thompson et al. 2020, Leibold et al. 2022).

A third, emerging perspective seeks organizing axes in terms of dynamical regimes. Inspired by statistical physics, this approach replaces the intractable microscopic details of specific interaction networks with summary statistics (Bunin 2017, Hu et al. 2022, Akjouj et al. 2024, Leibold & Barbier 2025). The success of this approach has motivated a novel organizational geometry defined by three orthogonal axes (Barbier 2025): the degree of randomness (spanning from order to stochastic processes), the strength of feedbacks (distinguishing linear causes from interaction-dominated dynamics), and the dynamical state (separating stationary regimes from transient behaviors). Unlike the process-based or scale-based classifications discussed above, which group models by their biological inputs, this framework organizes them by their emergent complexity.

To illustrate, consider how this cartographic approach clarifies the relationship between May's (1974) random matrix analysis and assembly-oriented coexistence models. May's experiment asked a sharply bounded question: If a community matrix is assembled by drawing interaction strengths at random, how does increasing species richness or connectance affect the probability that an equilibrium remains locally stable? On the axes of dynamical regimes, this places the model in a region of high randomness, weak feedbacks, and stationary dynamics: Interactions are unstructured draws, the analysis is linearized near equilibrium, and the focal outcome is local stability of a pregiven community. By contrast, assembly-oriented models ask a different question: How do communities form through sequential invasion, exclusion, priority effects, or disassembly when interaction structure is constrained by ecological mechanisms (Spaak & Schreiber 2023, Song 2025, Iwashita et al. 2026)? In such models, the object is not a random draw of a completed community matrix rather but a history-dependent trajectory through community states. Interaction signs and strengths are structured by competition, trophic position, or other biological constraints, feedbacks determine which species can invade or persist, and the outcome may be transient exclusion or alternative community composition rather than equilibrium stability alone. Plotted on the same axes, these theories are not rival answers to the same question. May's analysis identifies the null expectation for unstructured equilibrium communities; assembly models ask how ecological structure and invasion history generate the communities whose stability May's experiment deliberately bracketed. The apparent contradiction therefore becomes a division of labor.

Across these examples, the unifying theme is cartographic rather than prescriptive. The aim is to provide a coordinate system that renders diverse models legible to one another. By explicitly locating our theories—whether in terms of processes, scales, or dynamical regimes—it becomes easier to see which behaviors are generic, which are special cases, and where new theory is most needed. This shifts the collective task from defending individual fortresses to filling in the blank spots on the map.

6. THE HUMAN DIMENSION OF ECOLOGICAL THEORY

> New directions in science are launched by new tools much more often than by new concepts.
>
> —Freeman Dyson (1997)

The preceding sections treat theories as abstract objects: ways of formalizing ecological systems and functions that those models serve. In practice, however, theories are enacted by people. Theory does not live only in papers; it lives in software packages, on classroom whiteboards, and increasingly in the prompts of AI. Conceptual coherence in community ecology relies fundamentally on how these tools are distributed, taught, and used.

6.1. The Twin Barriers: Gatekeeping and Black Boxes

Many ecologists do not enter the field because they are drawn to mathematics. They arrive with motivations grounded in natural history, conservation, or environmental justice, often coupled with uneven quantitative preparation. Against this background, theoretical ecology can appear as a gated subculture with its own dialect and unwritten norms. When theory is presented primarily as a sequence of opaque derivations, or as a repertoire of canonical equations to be memorized, it reinforces the impression that formal work is reserved for an insular cadre of specialists (Grainger et al. 2022). This perception matters: It limits who feel authorized to ask theoretical questions and whose ecological intuitions are translated into models.

These sociological barriers interact dangerously with technical tools. The rise of user-friendly software for complex frameworks, while democratizing access, has inadvertently encouraged

"push-button" use. When a software function returns a value labeled "niche difference" or "stability index," it is tempting to treat this output as a direct empirical measurement rather than a conditional quantity defined within a specific, often restrictive, theoretical scheme. This decoupling of calculation from comprehension creates an "illusion of explanatory depth" (Rozenblit & Keil 2002): Analyses appear sophisticated, but they rest on unexamined assumptions about what is being measured and for what purpose.

6.2. Bridging the Gap: Intuition and Transparency

The field is actively developing remedies to bridge this divide. One strand of effort treats theory as a "second language" for empiricists, emphasizing geometric intuition over algebraic virtuosity. Seminal texts such as Case's (1999) *An Illustrated Guide to Theoretical Ecology*, alongside modern successors (e.g., Otto & Day 2011, Chisholm 2025), have paved the way. In parallel, a growing body of literature is explicitly demystifying core constructs, translating formal jargon into accessible concepts linked to experimental design (e.g., Grainger et al. 2022, 2025; Germain & Schreiber 2025; Song 2025).

Another strand research involves the creation of transparent, manipulable tools. Interactive platforms like EcoEvoApps allow users to vary parameters and observe dynamical responses in real-time (McGuire et al. 2022). Simultaneously, the growing mandate for open, annotated code is transforming reproducibility into pedagogy (Pick et al. 2026). When code is written to be read by humans, not just executed by machines, it exposes the formalization choices that otherwise remain hidden. These developments are turning abstract theories into exploratory objects that can be inspected, critiqued, and repurposed by the broader community.

6.3. Future Directions: AI and the Pivot to Verification

AI is already reshaping scientific practice, and ecological theory will not be exempt. The environmental costs of large language models are real and growing (Xiao et al. 2025), and the broader societal disruptions are genuine. Yet as scientists, we face a harder question than whether AI is good or bad: What happens to theoretical ecology if we refuse to engage with it seriously? Uncritical enthusiasm substitutes hype for evidence; uncritical dismissal forfeits any chance to shape how these tools are used. Neither stance is adequate. What is needed is what we, as ecologists, have always been trained to do: Examine the evidence, determine what works, identify what is broken, and act accordingly.

At present, many researchers use AI primarily for writing-focused tasks (Kusumegi et al. 2025), but the quantitative capabilities of these systems are advancing rapidly. As they do, their most transformative impact on theoretical ecology may lie not in automating what theorists already do but in democratizing who can participate in theoretical research.

For education, these tools offer something that used to be scarce: an "on-call expert" that can explain code, walk through derivations, and illustrate concepts interactively at the pace of the learner. For research, they function as a technical copilot, allowing empiricists to translate deep biological intuition into working code and stylized mathematical formulations with dramatically reduced friction (Wang et al. 2023). In the language of Amartya Sen (2009), AI expands the capabilities of ecologists, lowering the barrier between biological insight and formal expression.

However, this power comes with a profound risk: the automation of misspecification. Generative models can produce syntactically flawless code for ecologically incoherent models or supply persuasive verbal justifications for mathematical hallucinations (Messeri & Crockett 2024). If the black box of statistical software was dangerous, the black box of AI-generated theory is potentially more so, because it automates both the derivation and the justification.

This technological shift demands a fundamental pivot in how we train the new generation of ecologists. For decades, quantitative training has focused on derivation: teaching students to solve equations and write code from scratch. In an AI-augmented future, the scarce resource is no longer symbolic fluency, but critical scrutiny. We must shift training toward verification. The central question becomes not "Can I write the code for this model?" but "Do I know how to test if this model respects biological constraints and answers the right question?"

There is a genuine optimistic lens through which to view this shift. Analogous to the P versus NP problem in computer science, generating a solution to a complex problem is often hard, but verifying that a solution satisfies a set of constraints is computationally easier. If we train ecologists to be careful "verifiers" of models—using the kinds of diagnostics outlined in this review—then AI need not replace theoretical reasoning. Instead, it can help more people participate in it and make it easier to explore theoretical ideas that would otherwise be out of reach.

7. CONCLUSION: TOWARD A CONCEPTUAL COMMONS

> The only simplicity for which I would give a straw is that which is on the other side of the complex—not that which never has divined it.
>
> —Oliver Wendell Holmes Jr. [1961 (1902), p. 109]

The landscape of theories is densely populated in community ecology. Arguably, this is the inevitable consequence of studying a system as multiform and contingent as nature. However, the diversity that makes ecology vibrant also exacts a toll. It has become increasingly difficult to distinguish when theories truly disagree about nature, when they describe different facets of the same system, and when apparent conflict is merely a semantic artifact.

To navigate, I have proposed a diagnostic framework organized along two dimensions. Along the axis of formalization, distinguishing between model-driven and data-driven cultures reveals where structure enters our work—whether imposed a priori or discovered a posteriori—and identifies the distinct forms of misspecification that plague each. Along the axis of function, distinguishing between predictive heuristics, definitional frameworks, and theoretical experiments clarifies the intent of the models. This clarity helps prevent us from judging a heuristic by its mechanism, mistaking a definition for a falsifiable hypothesis, or dismissing a theoretical experiment for lacking forecasting skill.

Diagnosis paves the way to action. To turn pluralism into an asset, we must discipline how theories are built. On the side of formalization, I advocate for establishing shared benchmarks, enforcing fundamental constraints, advancing structural discovery to bridge the two cultures, and explicitly retiring outdated frameworks. On the side of function, I advocate for generalizing predictive heuristics to reveal their limits, actively translating definitional frameworks while acknowledging their irreducibility, and positioning theoretical experiments within explicit organizational axes to clarify their domains.

The unification of ecology is not merely a technical challenge but also a sociological one. Broadening access to theoretical tools through transparent code and concept-forward teaching has already lowered the barriers to entry. Additionally, the rise of scientific AI offers an unprecedented opportunity to further democratize access to theory. To harness this potential while guarding against its dangers, we must rethink quantitative training deliberately, shifting the emphasis from derivation alone to critical evaluation and verification.

Ultimately, ecology needs less of a grand unifying theory and more of a conceptual commons—functioning conversations across many imperfect theories. We must be brave enough to retire ideas that no longer serve us and, just as importantly, humble enough to recognize where opposing frameworks hold a piece of the truth. This review has charted that commons through the theories

of species interactions in community ecology, but the diagnostic framework extends to ecology at large. Ecological theories will remain what they have always been: love letters to Mother Nature that we may never fully grasp. But if we commit to moving from a Tower of Babel to a conceptual commons, we might, together, understand enough to keep her from unraveling (Parfit 2011).

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