Unfeasible expectations: why simple predictors outperform structural stability measures for understanding community assembly

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Abstract

Understanding what determines community assembly and disassembly in a changing environment is a core challenge for ecology. Recently a family of structural stability approaches that determine the range of intrinsic growth rates compatible with system feasibility have been gaining popularity as a measure of how likely a community is able to persist in fluctuating conditions. This offers a theoretical basis for understanding and predicting the assembly and stability of complex multi-species communities from only interaction network structures. However, here I show that the high sensitivity of calculations of the feasibility domain, coupled with empirical uncertainties inherent in estimated interactions, are likely to preclude the approach's reliable application to empirical settings. Across four reanalyses of previous empirical demonstrations of the structural stability approach, more parsimonious explanations based on species connectance provide better explanations for patterns of community assembly or dynamic stability. Calculation of structural stability metrics therefore appears to lose, rather than synthesise, information embedded in empirical interaction matrices. This success of simpler measures is good news for the purposes of prediction and emphasises the value of multiple-competing hypotheses in validation tests to demonstrate value-added associated with new approaches.

Introduction

Understanding the conditions and processes that determine the coexistence or otherwise of species is a central goal of ecology, but one that is hampered by the substantial, and inevitable, deficits in our empirical knowledge of species responses and interactions. The diverse and complex nature of ecosystems necessitates simplifying theoretical constructs to allow tractable analysis and progress to be made. A perennial challenge is how to best navigate the balance between pressures for increasingly detailed mathematical frameworks with the limitations of available empirical knowledge.

Recently the structural stability approach (Rohr *et al.* 2014; Saavedra *et al.* 2017) has been gaining ground as a tool in the quest for understanding and predicting both coexistence and assembly patterns of ecosystems. At its core, it takes an assumed matrix describing interactions between species under the framework of Lotka-Volterra models to calculate the diversity of population growth rates across the community that result in feasibility - all species having positive equilibrium biomasses. A relatively large feasibility domain implies that interspecific interactions impose relatively weak constraints as species can coexist at a larger number of growth rates combinations. As such, a community that has a larger feasibility domain is seen as relatively more stable. By contrast, a smaller feasibility domain implies that constraints are more rigid. This is frequently interpreted probabilistically as capturing the likelihood that a random combination of population growth rates result in a feasible community (Deng *et al.* 2024b; Song *et al.* 2020b).

Feasibility is often touted as a more ecologically relevant response variable than other options such as local asymptotic stability, and has been proffered as a means to understand the impact of external changes on communities given only knowledge of an interaction matrix (Allen-Perkins *et al.* 2023; Godoy 2019; Godoy *et al.* 2024; Saavedra *et al.* 2020). The approach can unite multiple strands of ecological thought (Godoy *et al.* 2018) and facilitates detailed analytic treatment of communities larger than the pairwise analyses possible under, say, classic Modern Coexistence Theory (Barabás *et al.* 2018). It allows the same framework to be used for both pairwise analyses (Song *et al.* 2020a) through to large communities (Grilli *et al.* 2017).

However, the standard structural approach is ultimately predicated on a given interaction matrix being a suitably accurate description of the interrelationships within the ecological community (Saavedra *et al.* 2020). Unfortunately, although the qualitative topology of the direct interactions between species may be (relatively) easily observed or be predicted from traits, quantitative interaction matrices are notoriously hard to even approximately parameterise (Wootton & Emmerson 2005). While tools for predicting interaction strengths from traits in aquatic and plant systems (Berlow *et al.* 2009; Freckleton & Watkinson 2001) have shown promise, accuracy still has a low ceiling. Furthermore, interactions frequently vary substantially through time (Ushio *et al.* 2018) as they are highly dependent on both the environmental (Chamberlain *et al.* 2014; Tylianakis *et al.* 2008) and biotic

conditions (Peacor & Werner 2004), making extrapolations from controlled conditions a considerable challenge.

Extreme sensitivity to the quantitative details of interaction matrices has been a hallmark of stability results using other metrics due to the rapid indeterminacy arising from chains of indirect effects (Novak *et al.* 2011; Yodzis 1988). Under the standard structural approach, the uncertainty and probabilistic interpretation are pushed onto the intrinsic growth rates, despite the observation that in many communities estimates of interaction coefficients are much more uncertain than intrinsic growth rates (e.g. Terry 2024). Given these challenges, it is therefore very notable that the structural stability approach has had multiple high-profile recent successes in describing the assembly of empirical communities (Bartomeus *et al.* 2021; Deng *et al.* 2024a; Domínguez-Garcia *et al.* 2024; García-Callejas *et al.* 2023; Medeiros *et al.* 2021; Saavedra *et al.* 2016; Song *et al.* 2018a; Tabi *et al.* 2020) despite often having access to only relatively crude approximations of interaction matrices, for example those generated from qualitative resource-use overlap approximations.

Ecological theory has many potential valid objectives (Grainger *et al.* 2021; Marquet *et al.* 2014; Shaw *et al.* 2024), but improved explanations of empirical data through predictions is certainly one of the most important components. However, identifying a correspondence with data can only a starting point of validating the utility of a theory. Ideally, a useful abstraction or theory should capture something additional and distinct to more parsimonious theories.

Here, I first demonstrate that even small empirical uncertainties in the interaction matrix can be expected to overwhelm any plausible signal of changes to a communities' feasibility domain and examine the challenges of propagating uncertainties to explore the consequences of focussing the uncertainty onto species growth rates. I then reanalyse four previous results to identify alternative simpler explanations for identified correspondences between inferred structural stability and observed community dynamics. I argue that, since apparent successes of structural stability are frequently exceeded by (or at the very least correlated with) simpler properties of the community, it may well be more profitable to focus on these simpler drivers. Ultimately this is a good news story, demonstrating the predictive information contained within even the relatively crude interaction networks available.

Calculation of a feasibility domain.

This section briefly summarises approaches to calculating the size of a feasibility domain ('Ω', or when scaled per species 'ω') given an interaction matrix **A**. To avoid simply repeating the many previous thorough treatments (e.g. Saavedra *et al.* 2017; Song *et al.* 2018b; Svirezhev & Logofet 1983), here the intuition is emphasised to keep the technical mathematical language to a minimum.

The population dynamics of each species (N_i) are assumed to follow Lotka-Volterra dynamics: $\frac{dN_i}{dt} = N_i\left(r_i + \sum_{j=1}^{n} \alpha_{ij} N_j\right)$, with intrinsic growth rates r_i and competition coefficients from species j on to

species i. However, it can also be applied to other similar models, such as alternative formulations of Lotka-Volterra (e.g. Tabi *et al.* 2020), nonlinear functional responses (Cenci & Saavedra 2018) or seed-bank models of plant dynamics (Song *et al.* 2021). This model can be written in matrix form and solved for equilibrium, $\mathbf{0} = \boldsymbol{r} + \mathbf{A}\boldsymbol{N}^*$. The equilibrium densities for a given community specified by $\boldsymbol{r}$ and $\mathbf{A}$, is then $\boldsymbol{N}^* = -\mathbf{A}^{-1} \cdot \boldsymbol{r}$. The fundamental question for a feasibility analysis is then, given only information on $\mathbf{A}$, what values of $\boldsymbol{r}$ would lead to all values of N_i^* being greater than zero?

The possible space of r_i values to search over is made easier by the observation that scaling the vector of r values wouldn't change the sign of $\boldsymbol{N}^*$. This means that each ratio of r values need only be tried once, which can be achieved by normalising the set of r's in some way. Approaches include the 'L1 norm' ($r_1 + \cdots + r_n = 1$) or more commonly the 'L2 norm' ($\sqrt{r_1^2 + \cdots + r_n^2} = 1$), which embeds the assumption that each ratio is equally likely and has the visually attractive property of forming a sphere in three dimensions (e.g. Fig. 1b).

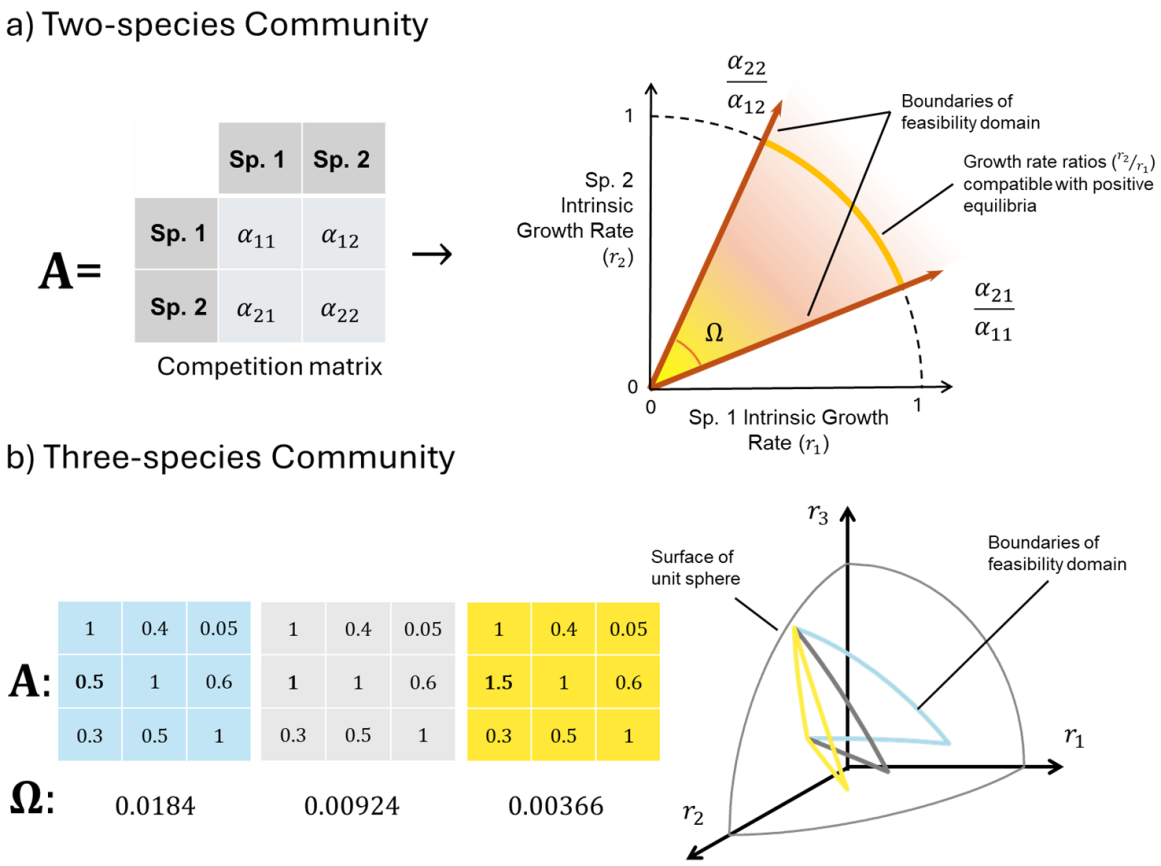

Figure 1. Illustration of calculation of feasibility domains for small communities. The objective is to calculate the proportion of combinations of growth rates (r) that are compatible with all species having a positive equilibrium ('feasibility'), given an interaction matrix $\mathbf{A}$ and assuming Lotka-Volterra dynamics. a) With two species, the boundary of the feasibility domain can be determined analytically, and the proportion Ω of feasible combinations of r is the angle between these boundaries. b) With three species, this angle becomes the triangular surface area on a sphere. Here three domains

corresponding to the three matrices are shown in three colours. Because all interactions are of the same sign, only one sector of the sphere is relevant. Note the large response in both the size Ω and location of the domain to a changing only a single element (α_{21}, in bold) by $\pm 50\%$. Beyond three species, the domain is no longer easily visualised, but the same principle applies.

With the Lotka-Volterra model, the possible r values that lead to feasibility make up a continuous 'domain', within definable boundaries. This feasibility domain can be summarised by both *which* vectors lie in the feasibility domain, and proportionally *how many* vectors. For two species, these boundaries, and hence the size of the feasibility domain Ω can be calculated directly (Fig. 1a). For more diverse communities, the calculation becomes a complex integral across each of the species. Fortunately, this can be computed through a quasi- Monte Carlo approach for fairly large communities (Genz & Bretz 2002; Saavedra *et al.* 2016). Effectively, this samples the proportion of a large number of trialled r-value combinations spanning the full range of possibilities that lead to feasibility. This proportion is denoted Ω (sometimes Ξ) and captures the *size* (although not the *location* or *shape*) of the feasibility domain. There also exist analytic approximations for large communities where the interaction strengths are identically independently distributed (Grilli *et al.* 2017).

Since with increasing species diversity, it tends to get harder to identify combinations of r that lead to feasibility, it is common to instead report this value scaled by the number of species n, $\omega = \Omega^{1/n}$. As such, ω can be interpreted as the average probability that a species will have a positive equilibrium value with a randomly drawn $\boldsymbol{r}$, making the chance of the whole community being feasible $\omega^n = \Omega$. The size of the 'possible' domain can be restricted to increase the biological meaningfulness, for example only considering positive r values in a competitive community, or negative values in a mutualistic one. These restrictions can scale the bounds of maximum feasibility.

It is worth noting that *feasibility* does not imply *stability* by default. Without even local stability feasibility on its own can't be taken to imply coexistence. However, feasibility is often associated with local stability in sampled systems (Case & Casten 1979; Roberts 1974; Song & Saavedra 2018; Stone 2018). Local asymptotic stability is much more likely with relatively strong intraspecific interaction strengths (Barabás *et al.* 2016, 2017) and can be guaranteed under certain conditions – for example the negative definite matrices studied by Grilli *et al.* (2017).

Sensitivity of Calculation of Structural Stability

Uncertainty in the estimation of feasibility domains enters in multiple ways with varying degrees of tractability. These considerations mean that 'probabilistic' interpretations of ω as the chance that a species will be able to persist given its interactions (Song *et al.* 2020b) must ideally account for multiple contributing factors: uncertainty in model structure, parameter uncertainty, environmental conditions, and potentially in the feasibility calculation itself. The core assumption is that the

interaction matrix **A** includes sufficient components (species) to capture the community dynamics of interest and that the network of interactions for a given spatial scale is stable enough through time to be summarisable as an interaction matrix. It also assumes that there is a good enough understanding of the functional form of the interactions to be able to meaningfully estimate interaction coefficients. Alternative plausible model forms can quite readily give alternative predictions (Cervantes-Loreto *et al.* 2023), somewhat confusingly in this context also termed structural sensitivity. However, since non-linear density dependence can (if some conditions are met, Cenci & Saavedra, 2018), be embedded in the same framework these impacts can to some extent be captured as uncertainty error in the competition matrix under the assumptions of the generalised Lotka-Volterra-like model. As a further complication, numerical calculation of feasibility becomes unstable when Ω is very small (in trials this tended to start to be noticeable above ten species), although this can be addressed by brute-force repeated calculation.

In a scenario where the underlying assumptions are considered reasonable, sensitivity analysis of the impact of perturbations to **A** are simultaneously a test of the impact of misidentification of measured interaction strengths and an analysis of a systems response to environmental changes affecting interactions. These are fundamentally different interpretations, but in an empirical application of the framework it is essential to separate the first from the second. While responsiveness to small changes is potentially an advantage in a tool, this is only the case if the underlying inputs are precisely measurable, something that is unfortunately not the case for ecological interaction networks (Wootton & Emmerson 2005). Even leaving issue of whether the underlying model is a suitable representation of the dynamics aside, it can be readily demonstrated with a virtual ecologist approach (Fig. 2) that even moderate error in elements of **A** causes such uncertainty in ω that a very large set of community comparisons would be necessary to convincingly identify a reliable signal through the noise. *Location* of the feasibility domain is even more sensitive than the *size* - in the example communities depicted Fig. 2b, there was no detectable overlap in the feasibility domain in any of the 100 pairs of observations, despite the 'observations' being much more precise than could be expected in any real network.

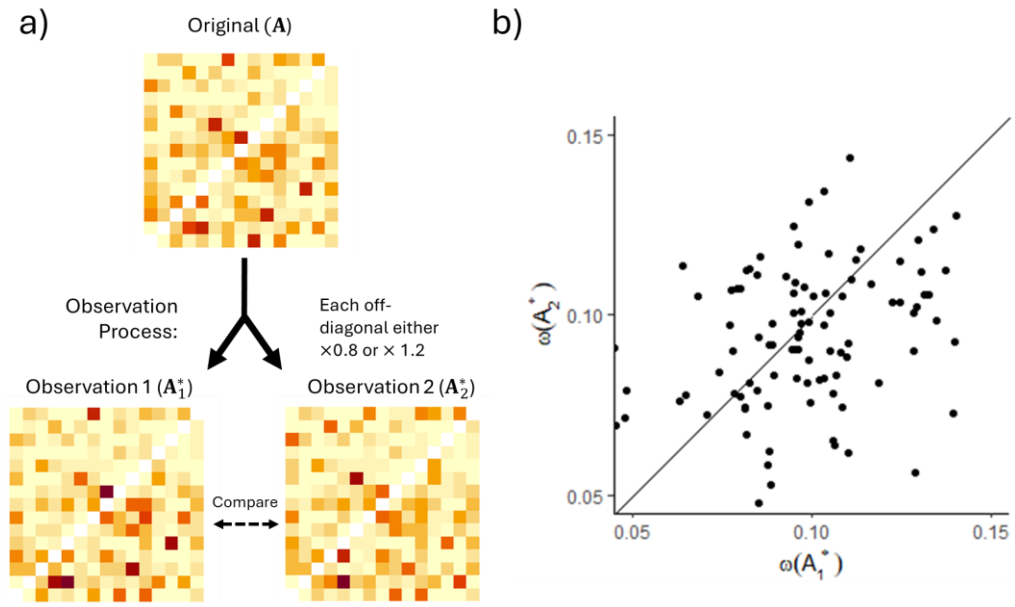

Figure 2. Demonstration of sensitivity of feasibility domain to specification of A. a) Comparison of repeatability of ω between pairs of 'observations' of original communities (species=15, connectance = 0.8, parameterised with a half-Normal) generated by randomly multiplying each off-diagonal element by either 0.8 or 1.2. As such 50% of interactions are identical between observations. This introduces weak noise while maintaining comparable fundamental properties of the matrices. Correlations between off-diagonal elements of the two observations ($\mathbf{A}_1^*$ and $\mathbf{A}_2^*$) averaged 0.93. (b) Results of 100 trials comparing repeat 'observations' of 100 different communities. Estimates of ω between the observations varied so considerably that no consistent signal can be discerned (ρ = 0.16).

The exact sensitivity to misspecification will depend on the structure of the community, calculable from the condition number (see e.g. Pomerantz 1981). However, it is well established that calculations involving inverting a matrix are highly sensitive (Barabás & Allesina 2015), with small eigenvalues of the matrix leading to particularly high sensitivity. Although the 'real' distribution of eigenvalues in communities is poorly known, the abundance of rare species frequently observed, suggests real ecological communities are highly sensitive (Barabás & Allesina 2015). As such, since the calculation of ω is based on the inverse of **A**, calculation of feasibility metrics will almost always magnify, rather than abstract across, errors in **A**.

Empirical two-species example incorporating empirical uncertainty.

Interpretation of 'virtual ecologist' power analyses are inevitably limited by the need to specify both the level of real variation to be discerned and the level of empirical noise. To give a more concrete example, it is therefore helpful to explore an example where empirical uncertainty was directly estimated. Fig. 2 illustrates an example using data from a comparatively well-characterised 2-species *Drosophila* mesocosm system described in Terry (2025). With high replication (thousands of observed

transitions across the two species) and a highly controlled environment, the precision of these parameter values is likely to represent a 'best-case' scenario. In this study, temperature-dependent competition models were selected and fit for two species with distinct thermal preferences. Competitive dominance was found to move from *D. pallidifrons* (Species 1) to *D. pandora* (Species 2) via a region of likely coexistence as the temperature increased. The fitted model and the posterior estimates for the parameters are given in Supplementary Information 2. Since the growth rates are known this is arguably not a scenario where structural stability would be considered a core tool (although see Song *et al.* 2021). However, the additional knowledge allows investigation of the application of the approach to cases where only interaction matrices are available. A pairwise case study allows easier visualisation of the challenges that are likely to be more problematic at higher dimensions.

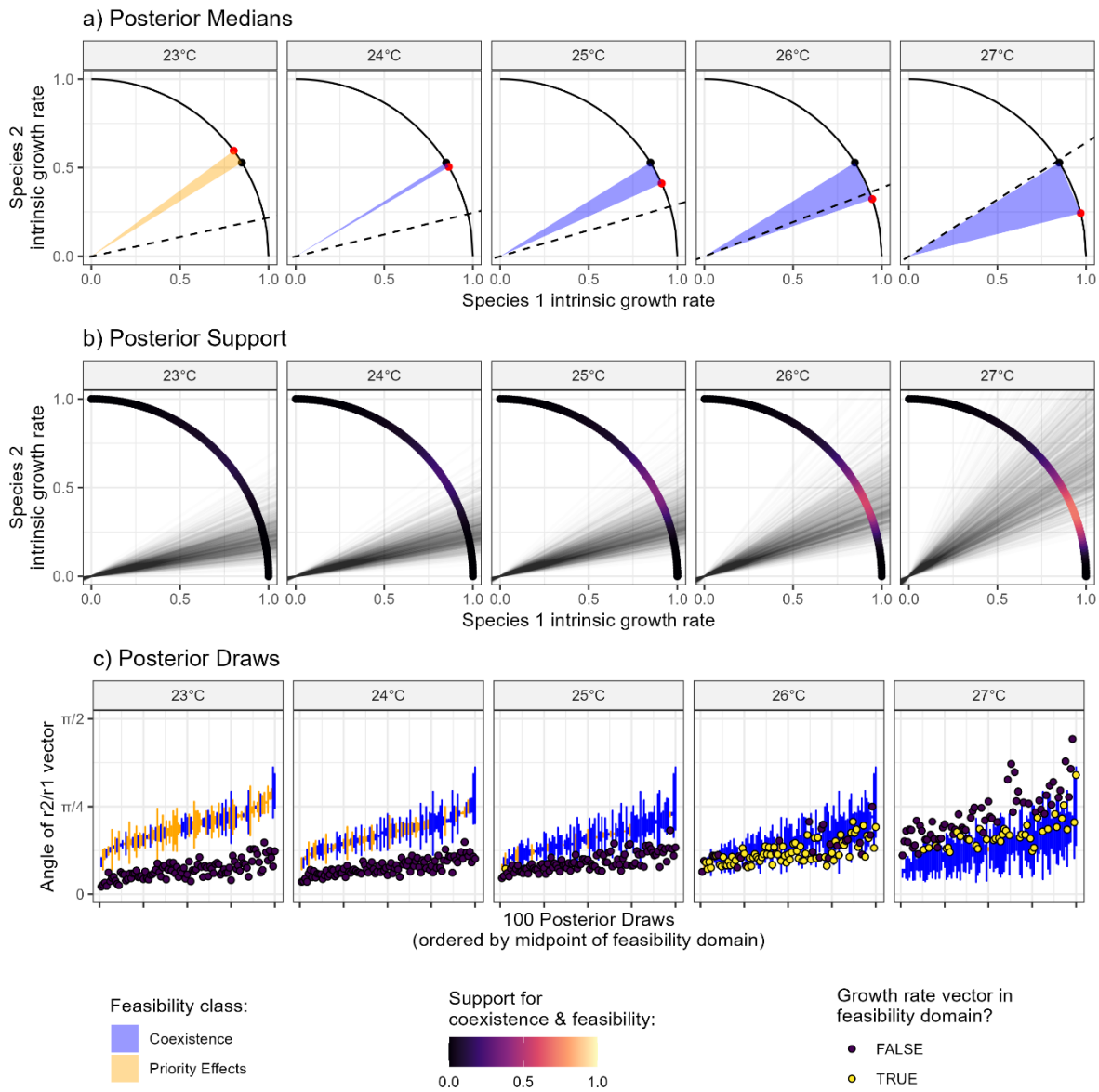

Figure 3. Feasibility domains of the competition between *D. pandora* and *D. pallidifrons* at five temperatures using fitted parameter posterior distributions. a) Feasibility domains using posterior median parameter values. Dashed line shows fitted intrinsic growth rate ratio. b) Support for each point on the unit sphere being part of the feasibility domain across the full posterior given by colour. Note that most points have low support for being contained in the feasibility domain. The fan of lines illustrates the posterior distribution of growth-rate vectors. c) Fitted growth rates are not independent of fitted competition terms. To illustrate this feasibility domains and growth rate vectors of 100 posterior draws are shown for each temperature.

A direct structural analysis making use of the posterior medians (Fig. 3a) would identify a marked rise in the size of the feasibility domain from 24°C with temperature. Note that there was only statistical support for identifying an impact of temperature on the α_{11} and α_{21} terms, hence only one of the feasibility domain boundaries responds to temperature. However, when considering the full posterior distribution of the parameter values, several challenges become clear:

Firstly, the *overlap* of feasibility domains from different draws of the posterior is at best moderate. In Fig. 3b, it can be seen that the support that any given community growth vector (r_2/r_1) is part of the identified coexistence feasibility domain is very rarely above half. Indeed, the overlap in feasibility domains varies more due to experimental imprecision than by an environmental change (+4°C) that was sufficient to reverse the outcome of competition. This poses a severe challenge to approaches that hope to measure the impact of environmentally driven changes from the overlap in feasibility domains (Godoy *et al.* 2024; Song *et al.* 2018b) as any such shift will likely be overwhelmed by even moderate empirical uncertainty. It would also be expected that the overlap of higher-dimensional feasibility domains between posterior draws would reduce faster in more diverse communities.

Second, the status of the feasible equilibria within the domain, i.e. whether stable coexistence or priority effects (Song *et al.* 2020a) are expected, is not necessarily consistent under parameter imprecision. Where the boundaries of the feasibility domain 'cross' ($\alpha_{21}/\alpha_{11} > \alpha_{22}/\alpha_{12}$, making niche overlap $\sqrt{\alpha_{21}\alpha_{12}/\alpha_{11}\alpha_{22}} > 1$), the interpretation of "feasibility" changes from stable to unstable equilibria. Different expressions to calculate the size of the feasibility domain implicitly deal with this challenge in different ways (Supplementary Information 1), but the widely used multivariate Gaussian sampling approach to measure Ω does not distinguish between the classes of "stability". A further consequence is that the size of the feasibility domain calculated from the median parameter values is identified as shrinking between 23°C and 24°C (to a very small value) while examining draws from the full posterior (Fig .3c) apparently shows an increase by averaging over draws containing both stable and unstable feasibility domains.

Lastly, but perhaps most crucially, despite these challenges around quantifying the feasibility domain's location and size, it is nonetheless clearly predicted that the feasibility domain would

enlarge with temperature. This would be interpreted as implying that coexistence of the two species was increasingly likely. However, this is the precise *opposite* of what is experimentally observed, where at high temperatures *D. pandora* is dominant (Terry 2025). Although there is increasing feasible space in the r_2/r_1 simplex at low values, at higher temperatures the observed r_2/r_1 vector moves more rapidly anti-clockwise through and *away* from this region (Fig. 3a). While this is clearly just a single example, it may well be expected that r-vectors of communities (particularly where the species have distinct environmental preferences) would change faster than changes in the size and location of feasibility domains, limiting their information value.

Re-evaluating Case studies & Alternative Explanations for Success

Recently there have been an increasing interest in extending the study of feasibility domains from a purely theoretical pursuit to empirical settings (Allen-Perkins *et al.* 2023; Saavedra *et al.* 2020). Multiple studies have identified relationships between the size of the feasibility domain and various measures of community assembly and stability, without the sample sizes that might be expected to be needed given the expectation of noise identified above. This is especially surprising given that many analyses are ultimately based on binary bipartite interaction matrices, from which are calculated (non-binary) effective interaction matrix based on inferred resource use overlap (Rohr *et al.* 2014, Fig. S1). While this approach has a long pedigree and makes best use of the available data (Godoy *et al.* 2018), it cannot be reasonably expected to generate **A**-matrices with the high levels of precision to give a dependable estimate of ω.

What then can explain the success? There are enough achievements to rule out luck or other bad faith explanations. Here I reanalyse four distinct studies that use empirical data of natural communities, in each case following as close as possible to the original objectives and approaches but testing if structural stability metrics are adding value compared to simpler species-level predictors that may offer plausible parsimonious explanations for the apparent success of calculated feasibility metrics as an explanation of community dynamics. These case studies were chosen based on having clearly tested empirical predictions, openly accessible data and as they had been repeatedly cited as providing an empirical justification for the use of structural stability metrics. R Markdown documents detailing all steps are available in the code repository.

Case Study 1 – Persistence of pollinator communities across sites.

In a large, 6-year, study within southern Spain, Domínguez-Garcia *et al.* (2024) found a strong ($\rho = 0.85$) positive correlation between the inferred structural stability ω of pollinator communities and average species persistence (as measured by the average proportion of years pollinators are observed in) across 12 sites. Here ω values were calculated based on effective interaction matrices for each site derived from plant resource overlap between the pollinators (Fig. S1). Site ω values are almost

perfectly correlated (ρ = 0.96, Fig. 4a) with the nestedness of each site's plant-pollinator network (calculated by the binary method of Bastolla *et al.* (2009) following the original paper). As might be expected given such a tight correlation, nestedness is indistinguishable from ω as a predictor of pollinator average persistence (Fig. 4b,c, 95% confidence intervals of Spearman's ρ_{ω}= 0.52: 0.978, $\rho_{nestedness}$ = 0.295:0.986), making it hard to distinguish with confidence the underlying driver. However, the original study also identifies moderate species-level correlations within each site between species-specific feasibilities (ω_i) and species persistence (ρ's between 0.37 and 0.66 for the 12 sites), which allows alternatives to be tested. Simply using the observed degree of each species within each site's network gives substantially higher within-site correlations with the observed persistence (ρ's between 0.706 and 0.93 for the 12 sites, Fig. 4d). Although the original study conducts network randomisations to identify that the specific network structure determines the calculated feasibility values, the process of calculating feasibility does not bring an identifiable gain of information at the community scale compared to the more empirically-robust nestedness metric (Nielsen & Bascompte 2007), and loses considerable predictive power at the species-level.

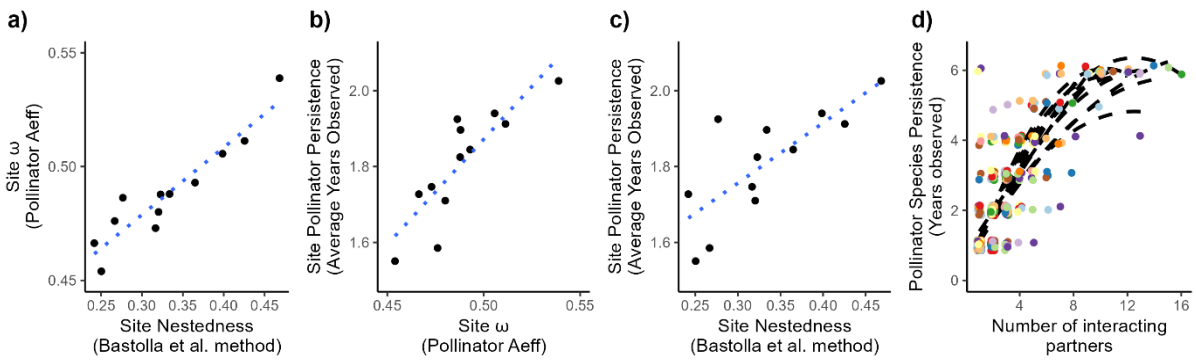

Figure 4. Reanalysis comparing binary nestedness or connectance with Ω as a predictor of pollinator persistence. In a-c, site level metrics are plotted, while in d points represent individual species coloured by site. a-c) Tight correlation between nestedness, the size of the feasibility domain and average persistence of pollinators as calculated by average years (out of 6) each species was seen in. d) At each site, how well does the number of interaction partners of each species predict the species-level persistence, calculated at the number of years (out of 6) that the pollinator was seen in. In all cases Spearman's rank correlations were used, fitted lines are shown to aid interpreation: a-c are linear model fits, while those in d) are quadratic lines of best fit and the points are jittered to reduce overlap.

Case Study 2 – Long-term Assembly of a Plant-Herbivore Community

Song *et al.* (2018a) examined how the assembly order of plant species into a large central European region (Baden-Württemberg, 35 751 km^2) affected herbivore community assembly, taking advantage of a large plant-insect interaction database (Altermatt & Pearse 2011) and estimated arrival times from

archaeobotanical and historical records. The observed binary interaction matrix was used to infer an effective competition matrix between insect herbivores that share the food plants present in the region, in each time slice between arrivals. After each set of plant arrivals, the herbivore competition matrix was recalculated and its ω calculated. They found a strong positive correlation between ω and time (Fig. 5a), and showed that this pattern was not simply an artefact of increasing diversity as it was reversed when the order of plant arrival was randomised. Moreover, the correlation was only seen in non-ornamental plants, while no such correlation was observed when focussing only on ornamental plants, suggesting a role for competition in community assembly. This was interpreted as the herbivore community being driven towards network structures with high overlap of host plant use during the early assembly stages, but this overlap diluted as the community developed.

However, reanalysing the data shows that a stronger trend can be identified from the observation that early arriving plant species tend to have more herbivores consuming them. Average vulnerability (number of herbivores linked to each plant) of the plants in the network in each time slice is highly correlated with time (Fig. 5b). Community average vulnerability and ω are highly correlated (Fig. 5c), but average vulnerability is more strongly negatively correlated with year (ρ = -0.932 [-0.955:-0.898]) than ω is correlated with year (ρ = 0.877 [0.818:0.917]), following the original paper in assuming independence of the time slices. The lack of a pattern with the ornamental plants is again retrieved (Fig.S2). Comparing the observed trajectory of average plant vulnerability though time with 1000x randomised arrival orders highlights the predictive power of this simple signal (Fig 5d). Since there is no comparable data on the arrival of the insect herbivores, the drivers of increased vulnerability of earlier arriving plant species is indeterminable, at least from this dataset. That said, the reanalysis suggests that the detected signal in feasibility of the herbivore community is readily explained by greater accumulation of enemies on earlier arriving plant species without needing to invoke community-level competition explanations at the regional scale.

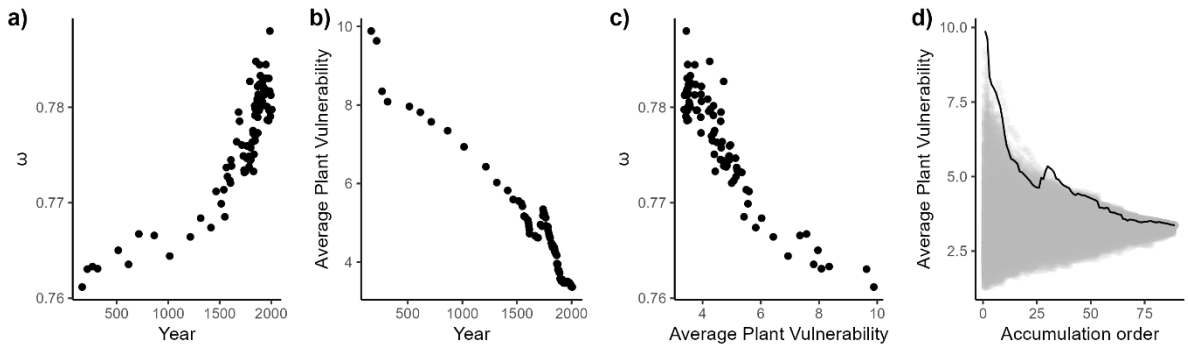

Figure 5. Reanalysis of relationship between plant arrival order into Baden-Württemberg and interactions with a lepidopteran herbivore guild. a) Original result of an increase in ω of the herbivore community through time. b) Strong and consistent decline in average links per plant (vulnerability) in the herbivore-plant network. c) Strong negative correlation between connectance

and ω. d) Observed trend in average plant vulnerability through time (black line) is markedly non-random when compared to 1000 randomised arrival orders (grey lines).

Case Study 3 - Species level feasibility domain metrics as a predictor of population dynamics.

Allen-Perkins *et al.* (2023) analyse data from Mediterranean annual plants to test whether species-specific metrics of the shape of the feasibility domain have the capacity to predict annual changes in the abundance of seven species across 5 year-year transitions. Specifically, they test the predictive capacity of a species 'exclusion ratio', a measure that compares the inferred size and shape of the feasibility domain to a null scenario where all species interact identically (García-Callejas *et al.* 2023). The larger a species' exclusion ratio, the greater the relative probability that it will be the first species excluded under a random environmental change.

The interaction matrices were calculated for each of seven years from independent data from fitted population models (García-Callejas *et al.* 2021). One year was excluded, generating 5 usable transitions. The original authors identified a negative relationship between the exclusion ratio of a species and its population growth rate ($\log_{10}(N_{t+1}/N_t + 1)$) , although this is not statistically significant (Fig. 6a). Across all observations Spearman's ρ was -0.096 (p-value = 0.58, n =35), following the original authors in treating the 5 observed transitions of 7 species as independent.

Given the diffuse competition networks, there is not a direct equivalent of linkage degree to tests as a basic predictor. However, a simple, if somewhat naïve as it does not consider the density of competitors, approach simply rowwise sums the interspecific elements ($\Sigma_j \alpha_{ij}$, for all $j \neq i$) of the interaction matrices to give an estimate of the competitive pressure felt by each species. This is able to give a markedly improved, although still statistically insignificant, explanation of observed abundance changes (Spearman's ρ= -0.299, p-value = 0.091, Fig.6b).

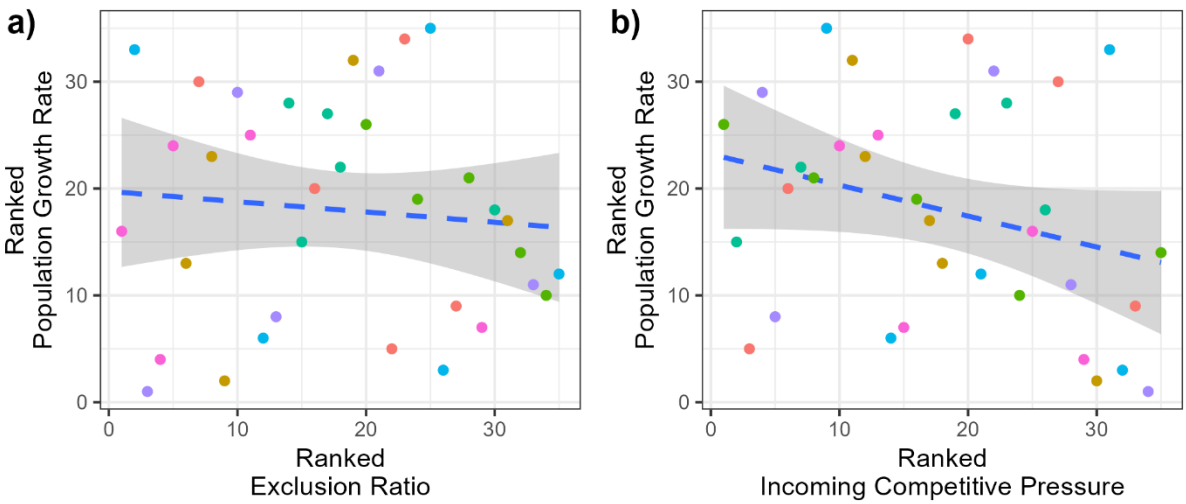

Figure 6. Comparison of explanatory power of species-specific structural stability-based metric to simple competitive pressure total for Mediterranean grassland plant dynamics. a) Replication of original result identifying link between species-level exclusion ratio feasibility-based metric that calculated the relative distance to the edge of feasibility domain for each species and observed annual population growth rate. b) Reanalysis using a (crude) estimate of incoming competitive pressure shows a stronger, although still insignificant, negative correlation. In both plots colours indicate different species and the line is a linear model (with 95% confidence intervals) fit through the ranks included to help visualisation.

Case study 4 – Observed combinations of herbivores through time across sites.

Medeiros *et al.* (2021) studied the community assembly of caterpillar herbivores across tropical dry forest sites at three successional stages (Boege *et al.* 2019). For each of 88 sampled communities an effective competition matrix **A** between herbivores was constructed based on species occurrences within a plot and a binary meta-network of plant-caterpillar interactions. The Ω of this matrix was calculated and compared to a distribution of $\Omega(\mathbf{A})$ calculated from equally sized herbivore communities drawn at random from the regional species pool. They found strong support that the observed communities had a larger Ω than would be expected from random draws, and inferred that observed communities are those more likely to persist in the face of changing environmental conditions (Fig. 7a). However, a much stronger signal is seen with a considerably simpler connectance based approach (Fig. 7b). Observed plant-herbivore connectance was much higher than random, and was much more statistically significant than the feasibility domain signal. In fact, in half of the communities, the observed community had a higher connectance than all 10’000 randomly drawn communities. Patterns in community assembly can in this case be directly explained simply by the over-representation of generalist species at each site.

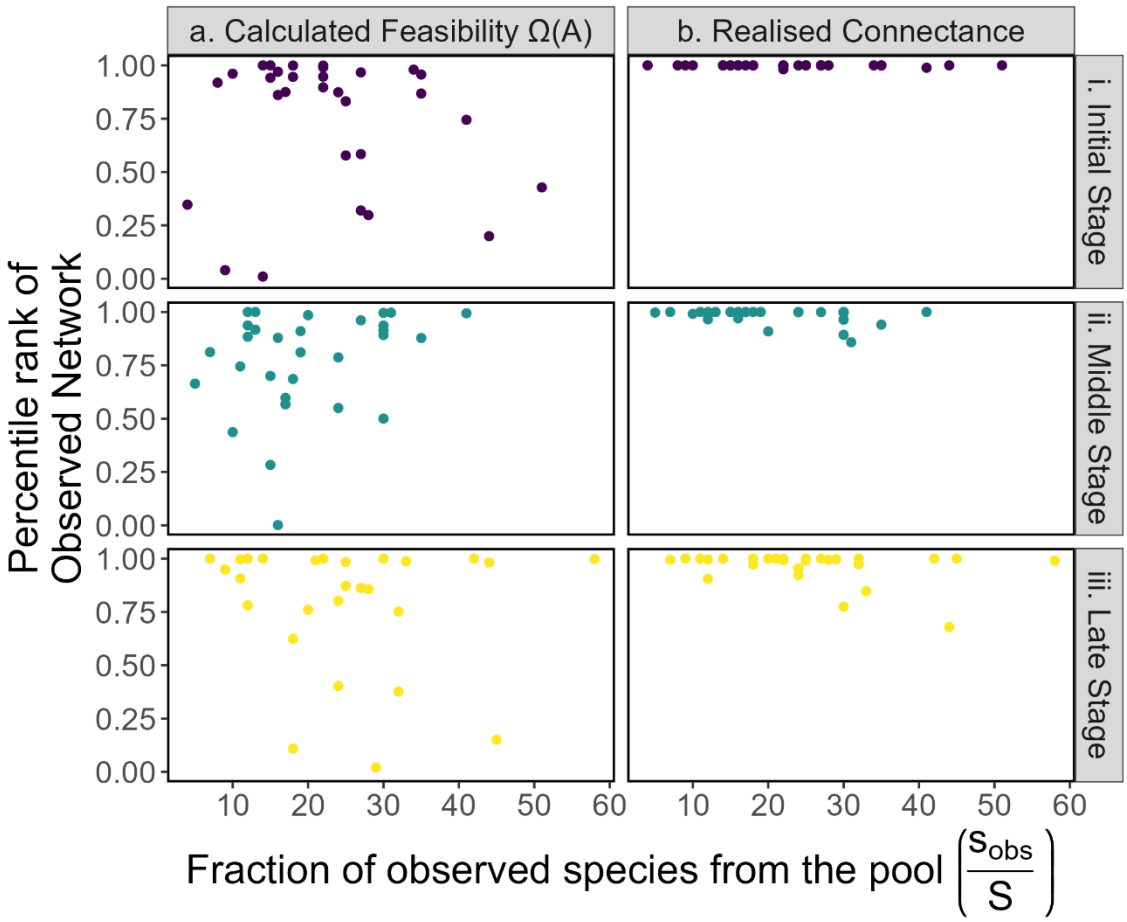

Figure 7. Comparison of properties (calculated feasibility domain and connectance) of observed tropical forest networks to randomly assembled communities. While estimated feasibility was significantly higher than would be expected under a random scenario (a), the signal from simple connectance was much stronger (b). This held true across a wide range of proportion of observed species (x-axis). Split of the communities into three stages and on the x-axis by the relative diversity of possible species seen in each community follows the original paper.

Revaluating the relationship between community dynamics, Ω and network structure.

The bi-directional relationship between community structure and dynamics has a long and complex history, bedevilled by the multitude of measures of both (Dunne & Pascual 2006). Given the assumptions underlying the methodology and uncertainties in the underlying interaction matrices, calculated values of ω are unlikely to actually represent the theoretical quantities they purport to, yet might still have predictive power. This has potential consequences for the long-running discussion regarding the relationship between dynamics, feasibility and network structure (Aparicio *et al.* 2023; Bastolla *et al.* 2009; Blüthgen & Staab 2024; James *et al.* 2012; Rohr *et al.* 2014; Saavedra *et al.* 2016; Saavedra & Stouffer 2013; Suweis *et al.* 2013; Valdovinos *et al.* 2016). Rather than feasibility explaining the apparent dominance of certain network structures (such as high generality or

nestedness), these results suggest causation appears as, if not more, likely to be the other way – the inferred ω values of observed networks are higher because something about their underlying structure leads to higher calculated ω values and higher likelihood of being observed as a community (Fig. 8). For example, García-Callejas *et al.* (2023) showed how inferred feasibility is closely driven by intraguild interaction overlap and average diagonal dominance across 18 communities. Observed networks have degree distributions that appear to maximise structural stability (Domínguez-Garcia *et al.* 2024). These relationships offer an explanation for how structural stability has been able to generate accurate predictions despite uncertainties in the input matrices and contexts where the fine detail of network structure is likely to play a subsidiary role in determining dynamics.

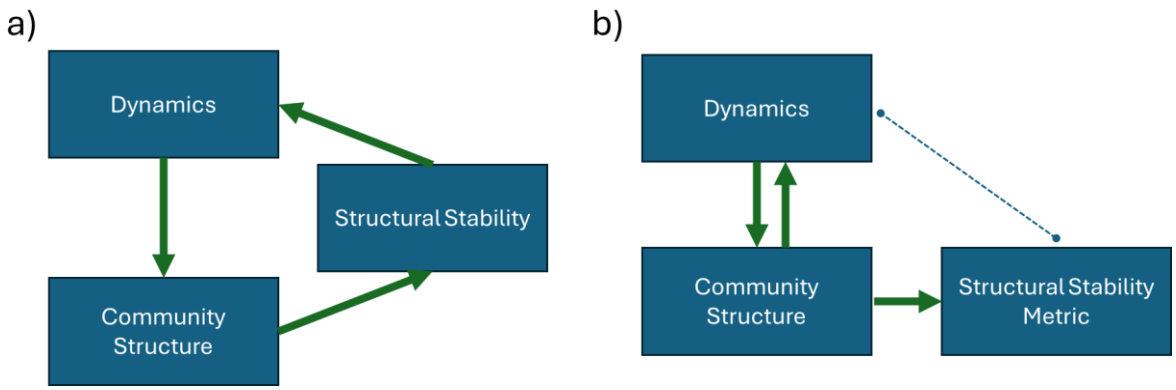

Figure 8. Alternative interpretations of observed correlations between structural stability and community assembly patterns. a) Structural stability could be synthesising something fundamental about the community structure that is a core driver of the dynamics of the ecological community. b) The structural stability metrics could be driven by elements of community structure that influence dynamics through some other mechanism, resulting in correlation without causation.

Increasingly, feasibility domain measures such as ω have been used as a stand-in response variable for describing the dynamic impact of network structure when actual dynamic data is not available (e.g. Arroyo-Correa *et al.* 2023; De Laender *et al.* 2023; Dougoud *et al.* 2018; García-Callejas *et al.* 2023; Rohr *et al.* 2014), a use that has been justified by its the apparent explanatory power in empirical tests. However, the weaker relationship to observed dynamics than simpler, more direct, metrics suggests that in empirical scenarios ω is often better thought of as a (noisy) descriptor of network 'structure', rather than an emergent dynamic response. Identifying the direction of causation between measures and importance is an important question - structural considerations such as feasibility may well be part of the deeper explanation for why connectance based metrics are able to perform well. It appears that ω is frequently a relatively inefficient summary of other network properties, and an overreliance of it as a response variable it may well distract from features, like basic connectance, that may be considerably more interpretable.

Conclusion and Outlook

Structural stability and the analysis of feasibility is an inherently attractive approach, linking scales and ecological processes while apparently needing minimal information and unlocking a set of sophisticated analysis tools. It is crucial to stress that these case studies are not at all a rejection of the concept of feasibility as a theoretical tool for generating explanations for the patterns we observe in nature. Rather, they suggest that the precision required appears to be effectively empirically unattainable and that apparent successes need to be interpreted with more scepticism. If methods of generating interaction matrices from bipartite observations of interactions are effectively repackaging that qualitative structure in a pseudo-quantitative form, a key future question for future research is what can the calculation of feasibility add on top of other metrics?

It is well understood that the Lotka-Volterra assumptions necessary to calculate structural stability exclude numerous important processes that operate at the community level (Levine *et al.* 2017; Levins 1968). When studying complex, ever-changing, ecological communities, there will always be a fundamental gulf between the simplifications necessary to generate analytic results and the known complexity of real ecological systems (May 1973). Better connecting theoretical and empirical results must remain a driving objective, but the difficulty of the challenge means that the identification a correlation between abstract theoretical results and empirical observations has to be the start, not the end, of the road of identifying the utility of a framework.

The challenges of developing and testing theories around the role of species interactions in community assembly is well-trodden ground (e.g. Quinn & Dunham 1983; Roughgarden 1983; Simberloff 1983). Given the multi-causal, integrative, nature of ecology (Hilborn & Stearns 1982; Siegel & Dee 2025), explanations and contributing factors are often tightly interwoven and need to be carefully unpicked to form a firm basis for further work. This of course, is much easier said than done (Betini *et al.* 2017) but a key step to identifying if the assumptions and simplification are inherent within a particular framework are useful is comparing the explanatory power of an approach to alternative, more parsimonious, explanations. Until such a signal is demonstrated, the utility of assuming measures of ω equate directly to the 'likelihood of community persistence', without further qualifiers, may be doubtful.

Moving forward, more explicitly accounting for parameter uncertainty in calculations is a basic start (Barabás *et al.* 2014; García-Callejas *et al.* 2023; Simmonds *et al.* 2022; Terry & Armitage 2024), but hits fundamental barriers discussed earlier and may well not be enough to head off more fundamental uncertainties inherent within the structural approach (Cervantes-Loreto *et al.* 2023). Analyses need to be clear exactly which contributors to uncertainty (model, parameters, environment, interaction structure, feasibility calculation etc) are being propagated, and how far through the analysis such uncertainty is carried through, to ensure error bars are interpreted appropriately (Simmonds *et al.* 2024). Causal inference techniques (Siegel & Dee 2025) can start to unpick the cause and effect of

interrelated measures of community structure and dynamics, but will be restricted by the small effective sample size of comparable networks. Shifts in the scale of communities analysed could also be productive - analyses focussing on smaller compartments of communities can allow higher accuracy with less scope for cascading dependences, but this cannot address dynamics of more complex communities. For large communities without very strong structure that meet stability criteria, feasibility is well determined by macro-properties of the community (such as connectance, mean interaction strength and variance, Grilli *et al.* 2017). By moving beyond the need for exact specifications of the interaction network, at larger scales there is scope to greatly reduce problematic over-sensitivity (Barbier *et al.* 2018).

Ultimately, the result that simple measures that don't require detailed knowledge of the whole network can better explain community assembly can be interpreted as positive news for addressing the challenges of a changing world that ecologists hope to address. While building more synthetic and wider-scope whole-network level metrics should remain a goal, local-scope, species-level, measures have much more directly explainable impacts which are more robust to uncertainty and are easier to scale up. They should not be neglected as a baseline from which to build a more holistic understanding of ecological dynamics.

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