The feasibility principle in community ecology

Serguei Saavedra[1,2*]

[1] *Department of Civil and Environmental Engineering, MIT,*
77 Massachusetts Av., Cambridge, MA 02139, USA

[2] *Santa Fe Institute,*
Santa Fe, NM 87501, USA

[*] *To whom correspondence should be addressed. E-mail: sersaa@mit.edu*

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Abstract

The structure and function of ecological communities emerge from interactions among populations within specific environmental contexts. Yet we still lack general principles that explain how communities assemble, which patterns we should expect, and when transitions occur across diverse settings. To address this challenge, I propose the feasibility principle in community ecology as a guide to assembly. Grounded in a synthesis of theoretical work and empirical studies, the principle is articulated through three hypotheses: (i) for a given interaction structure at a given time, each potential community has a feasibility domain—the range of environmental conditions under which it can persist; (ii) during assembly, the communities most likely to be observed are those whose feasibility domains overlap most with local conditions; and (iii) transitions among communities occur when environmental change or species gains and losses move the system across boundaries separating their feasibility domains, with the probability of a transition decreasing as the overlap between the corresponding domains becomes smaller. This framing focuses on feasibility domains and the boundaries that separate attainable communities, providing testable predictions for assembly and transitions without invoking a particular dynamical endpoint. I outline a quantitative framework to estimate feasibility domains and compare predictions with data across organisms and contexts. In the face of rapid climate change and habitat modification, I discuss how the feasibility principle can inform conservation and restoration by anticipating assembly pathways, likely transitions, and points of intervention.

KEYWORDS: assembly | interactions | feasibility | emergence | transitions | probability

> *"For science, there are many possible worlds; but the interesting one is the world that exists and has already shown itself to be at work for a long time. Science attempts to confront the possible with the actual" François Jacob (Jacob, 1994)*

A long-standing question in ecology is whether general principles characterize the adaptability and evolvability of biological populations, irrespective of organismal type or environmental context (Alberch, 1991, Levins, 1968, Lotka, 1920, Margalef, 1968, Parisi, 1999, Volterra, 1926). Identifying such principles would substantially advance our understanding of the processes that organize biological systems above the population level (Flack, 2017, May and McLean, 2007*b*, Odum, 1969, Solé et al., 2024). In community ecology, diversity within and among communities is widely viewed as an emergent outcome of interactions among populations embedded in specific environments (Morin, 2011, Pascual and Dunne, 2005, Solé and Bascompte, 2005, Vellend, 2016). Yet we still lack common principles that explain how communities assemble and reassemble, which patterns should be expected, and when transitions occur across varying environmental conditions (Marquet et al., 2014). Uncovering such principles would also provide actionable guidance for conservation and restoration aimed at mitigating the detrimental effects of anthropogenic change on biodiversity (Lenton et al., 2021, Levin, 1999).

Community assembly has been framed by a set of complementary processes. Environmental filtering holds that species whose functional traits match local conditions are more likely to establish and persist (e.g., Keddy, 1992, Kraft et al., 2015, Weiher and Keddy, 1995). Limiting similarity and niche partitioning posit that coexistence requires sufficient differences in resource use or performance, leading to predictable "packing" along niche axes (Abrams, 1983, Chesson, 2000, MacArthur and Levins, 1967, Tilman, 1982). Trade-off principles—such as competition–colonization or defense–growth—explain sequences of replacement and coexistence in disturbed or spatially structured habitats (Levins and Culver, 1971, Tilman, 1994). At broader scales, metacommunity theory formalizes how selection, drift, dispersal, and diversification jointly shape composition via species sorting, mass effects, patch dynamics, and neutral processes (Hubbell, 2001, Leibold and Chase, 2017, Leibold et al., 2004, Vellend, 2010). Historical contingency and priority effects show that arrival order can steer systems toward alternative but defensible endpoints under the same conditions, sometimes reinforced by eco-evolutionary dynamics (De Meester et al., 2016, Drake, 1991, Fukami, 2015). In parallel, work on transient dynamics emphasizes that communities can spend long periods away from equilibrium, with implications for inference and intervention (Hastings, 2001). A network perspective further demonstrates that the topology and strengths of species interactions constrain which assemblages are attainable, with insights from structural stability analyses, random Lotka–Volterra models, and sensitivity analyses (Barabás et al., 2014, Barbier et al., 2018, Bunin, 2017, Saavedra et al., 2017*b*, Serván et al., 2018). These lines of research suggest points of contact and motivate the search for common principles driving the assembly of ecological communities.

Taken together, these perspectives point to a common organizing idea: which assemblages occur, and when they change, depends on how interaction structure fits local conditions. Building on this idea, I propose the *feasibility principle* in community ecology. This principle is rooted in a *structuralist perspective* (also known as the internalist perspective) (Alberch, 1989, Kirschner and Gerhart, 2005, Solé et al., 2024), which holds that changes in the state of a living system are catalyzed by external perturbations within an environmental space, but whose effects are constrained by an internal structure of interactions among the system's components (Alberch, 1991). For instance, phenotypic expression may depend on a combination of morphogenetic parameters and genotypes, some environmentally invariant (i.e., internal constraints) and others environmentally variable (i.e., influenced by external factors). From this premise, the feasibility principle rests on three core hypotheses: (i) for a given, time-specific interaction structure, an ecological community possesses a feasibility domain—the range of environmental contexts in which it can persist; (ii) the probability of observing a given community increases with the portion of its feasibility domain that is compatible with local environmental conditions; and (iii) the probability of transitioning between two communities decreases as the overlap between the portions of their feasibility domains compatible with local conditions becomes smaller. I outline below how this principle can be formalized within a quantitative framework and empirically evaluated across a broad range of taxa and ecosystems. In the context of accelerating climate change and widespread habitat alteration, I further explore how the feasibility principle can inform assessments of ecological robustness and guide efforts in community restoration.

Feasibility and structuralism. From a quantitative standpoint, feasibility in community ecology is the existence of a real, strictly positive solution—typically, positive population densities—within an ecological model. This condition implies the possible long-term persistence of a system $\mathcal{S}$ composed of n interacting populations (Case, 2000, Gilpin, 1975, May and McLean, 2007*a*, Vandermeer and Goldberg, 2013). Importantly, such persistence does not necessarily entail dynamical stability—that is, a tendency to return to equilibrium after small perturbations in densities (Allesina and Tang, 2012, Song et al., 2020, Song and Saavedra, 2018, Vandermeer and Goldberg, 2013). A common representation is

$$\dot{N}_i = N_i\, f_i(N), \qquad i = 1, \ldots, n,$$

where $\dot{N}_i$ is the time derivative of density N_i, the functions f_i are per-capita growth rates (often low-order multivariate polynomials), and $\mathbf{N} = (N_1, \ldots, N_n)^\top$ (Arditi et al., 2021). Under this framework, feasibility corresponds to the existence of at least one equilibrium $\mathbf{N}^* = (N_1^*, \ldots, N_n^*)^\top$ with $N_i^* > 0$ for all i and $\dot{N}_i = 0$ (equivalently, $f_i(\mathbf{N}^*) = 0$) for all i. If at least one component is zero (e.g., $\mathbf{N}^* = (N_1^* > 0, \ldots, N_{n-1}^* > 0,\, N_n^* = 0)^\top$), the solution lies on the boundary of the nonnegative orthant and is termed a boundary equilibrium. Including boundary equilibria allows analysis of partial feasibility, that is, the feasibility of specific subsets (communities) $\mathcal{C} \subseteq \mathcal{S}$ within a larger species pool ($\mathcal{S}$). This definition provides a basis for assembly by linking which communities are attainable to how local environmental conditions position the system relative to their feasibility sets.

Traditionally, feasibility conditions—typically expressed as inequalities involving model parameters—are obtained by identifying the isoclines $f_i(\mathbf{N}^*) = 0$ for all $i \in \mathcal{S}$ and solving for the equilibrium vector $\mathbf{N}^*$. Feasibility is then established by imposing $\mathbf{N}^* > \mathbf{0}$, ensuring that all equilibrium population densities are strictly positive (AlAdwani and Saavedra, 2022, Case, 2000, Vandermeer and Goldberg, 2013). One of the most analytically tractable frameworks for conducting this analysis is the generalized Lotka–Volterra (gLV) model (Case, 2000, Lotka, 1920, Takeuchi, 1996, Volterra, 1926), which describes the temporal dynamics of interacting populations through a system of ordinary differential equations:

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^{n} a_{ij} \, N_j \right), \qquad i = 1, \dots, n.$$

Here $N_i(t)$ is the density (or biomass) of population i, r_i is its effective growth rate, and a_{ij} is the per-capita effect of population j on i. The effective growth rate r_i aggregates intrinsic biological properties and unmodeled environmental influences (abiotic and biotic). A negative r_i indicates a growth deficit in the absence of interactions (e.g., for obligate consumers), whereas a positive r_i indicates a growth surplus (e.g., for primary producers) (Odum and Barrett, 2005, Pielou, 2001). By contrast, the coefficients a_{ij} capture the explicitly modeled biotic interactions—often linked to bioenergetic transfers or mass conservation—among populations in $\mathcal{S}$. Thus, the gLV model separates direct environmental effects (through the r_i) from internal system interactions (through the a_{ij}), offering a mechanistic yet phenomenological representation of community dynamics. Moreover, the gLV equations have a strong theoretical foundation: they can be derived from principles of thermodynamics, mass and energy conservation, and chemical kinetics in the limit of large population sizes (Logofet, 1993, Lotka, 1920, Michaelian, 2005, Täuber, 2011). This grounding makes the gLV framework a natural tool for analyzing feasibility and persistence, and for defining feasibility domains in the space of growth-rate parameters r that I use below to develop forward-looking predictions about community assembly.

More generally, let $\mathbf{u}$ (e.g., $u = \mathbf{r}/\|\mathbf{r}\|$) denote the environmental direction and let $\Sigma \subseteq \mathbb{S}^{n-1}$ be the set of locally realized directions with density $p(\mathbf{u})$ on the unit sphere (see Appendix). For any community $\mathcal{C} \subseteq \mathcal{S}$, its feasibility domain $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ is the set of directions $\mathbf{u}$ for which the equilibrium on $\mathcal{C}$ satisfies $\mathbf{N}^*_{\mathcal{C}}(\mathbf{u}) \gg 0$. Here, subscripts $\mathcal{C}$ indicate restriction of vectors/matrices to the indices in $\mathcal{C}$. For absent species, the stationarity condition holds trivially because $\dot{N}_j = N_j(\cdots)$ and $N_j^* = 0$. When arrival order matters, historical contingencies are encoded by a selection function $h_{\mathcal{C}}(\mathbf{u}) \in [0, 1]$ giving the probability that $\mathcal{C}$ is realized among the admissible candidates under direction u, with $\sum_{\mathcal{C}} h_{\mathcal{C}}(\mathbf{u}) = 1$ for almost every—except on boundary/tie sets of measure zero—$\mathbf{u} \in \Sigma$ (see Appendix). Throughout I take $p(\mathbf{u})$ to be a probability density on Σ (i.e., $\int_\Sigma p(\mathbf{u})\, d\mathbf{u} = 1$) and interpret the expression below as a conditional probability given $(\mathbf{A}, \Sigma, p, h)$:

$$\mathbb{P}(\mathcal{C} \mid \mathbf{A}, \Sigma, p, h) \;=\; \int_{\Sigma \cap D(\mathcal{C},\mathcal{S},\mathbf{A})} p(\mathbf{u})\, h_{\mathcal{C}}(\mathbf{u})\, d\mathbf{u},$$

which marginalizes over environmental directions $\mathbf{u}$ and allocates among admissible endpoints via $h_{\mathcal{C}}(\mathbf{u})$. For brevity, one can write $\mathbb{P}(\mathcal{C})$ when the conditioning is clear from context. This expression separates environmental support from history: the intersection $\Sigma \cap D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ implements the impossibility filter and sets an upper bound on frequency, whereas $h_{\mathcal{C}}(\mathbf{u})$ redistributes probability where multiple endpoints are admissible. Under randomized or unbiased introductions, $h_{\mathcal{C}}(\mathbf{u})$ is approximately uniform across admissible candidates, so relative frequencies are predicted by feasible overlap alone.

Hypothesis 1 (existence of a feasibility domain). A community $\mathcal{C} \subseteq \mathcal{S}$ is feasible over a *set* of environmental contexts constrained by its internal structure (Fig. 1). In other words, for any given interaction structure, there exists at least one possible world—empirically observable or theoretical—in which $\mathcal{C}$ can persist. This claim is *model-independent*: it refers to the compatibility between external forcing and internal constraints and does not hinge on the assumptions of a particular dynamical formalism (Solé et al., 2024).

Within the gLV framework, feasibility is determined by the *direction* of the effective growth-rate vector, $\mathbf{u} = \mathbf{r}/\|\mathbf{r}\|$. For a fixed interaction matrix $\mathbf{A}$, the equilibrium on $\mathcal{C}$ satisfies $\mathbf{r}_{\mathcal{C}} + \mathbf{A}_{\mathcal{C}\mathcal{C}}\mathbf{N}^*_{\mathcal{C}} = 0$, hence $\mathbf{N}^*_{\mathcal{C}}(u) = -\,\mathbf{A}^{-1}_{\mathcal{C}\mathcal{C}}\mathbf{r}_{\mathcal{C}} = -\,\|\mathbf{r}\|\,\mathbf{A}^{-1}_{\mathcal{C}\mathcal{C}}u_{\mathcal{C}}$. Because multiplying $\mathbf{r}$ by any positive scalar only rescales $\mathbf{N}^*_{\mathcal{C}}$, feasibility depends on $\mathbf{u}$ (its direction) and not on $\|\mathbf{r}\|$ (its magnitude) (Grilli et al., 2017, Rohr et al., 2014, Saavedra et al., 2016*b*). The classification of parameters as environmental (contextual) or structural can vary across models (Flores-Arguedas et al., 2023), but the conceptual split between external drivers and internal constraints is general. Mathematically, there is a linear correspondence between equilibria and parameter configurations: for any feasible equilibrium $\mathbf{N}^*$, there is a unique direction $\mathbf{u}$ such that $\mathbf{r} = -\,\mathbf{A}\,\mathbf{N}^*$ and $\mathbf{u} = \mathbf{r}/\|\mathbf{r}\|$ (Medeiros et al., 2021*b*, Rohr et al., 2016, Saavedra et al., 2017*b*).

More generally, the corresponding set of directions $\mathbf{u} \in \mathbb{S}^{n-1}$ that render $\mathcal{C}$ feasible—given an internal structure $\mathbf{A}$ and species pool $\mathcal{S}$—defines its *feasibility domain*, denoted $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ (Logofet, 1993, Saavedra et al., 2017*b*, Song et al., 2018*b*). This domain characterizes the range of environmental directions compatible with the long-term persistence of $\mathcal{C}$ and underpins Hypothesis 1. Conceptually, it expresses biological redundancy: the same internal structure may be compatible with multiple environmental contexts (Waddington, 1942). Practically, $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ is the map of attainable communities for a given interaction structure; movements of $\mathbf{u}$ within or across these domains forecast which assemblages can persist and when transitions are expected, and the set can be explored systematically across the 2^n possible subsets (including boundary-equilibrium cases) (Deng et al., 2021, 2022).

Hypothesis 2 (observability scales with feasible local contexts). Holding the internal structure fixed, the probability of observing a community $\mathcal{C} \subseteq \mathcal{S}$ at a site is proportional to the amount of locally realizable directions that render $\mathcal{C}$ feasible (Fig. 1).

For each environmental direction $\mathbf{u}$, let $\mathcal{E}(\mathbf{u})$ be the set of *admissible endpoints*: communities that are feasible under $\mathbf{u}$ and *resist establishment* by any missing species (non-invasibility, see Appendix). Define $k(\mathbf{u}) = |\mathcal{E}(\mathbf{u})|$. Under neutral history, one can take $h_{\mathcal{C}}(\mathbf{u}) = 1/k(\mathbf{u})$ for $\mathcal{C} \in \mathcal{E}(\mathbf{u})$ and $h_{\mathcal{C}}(\mathbf{u}) = 0$ otherwise. Then, the neutral-history prediction is

$$\mathbb{P}(\mathcal{C}) \;=\; \int_{\Sigma\cap D(\mathcal{C},\mathcal{S},\mathbf{A})} \frac{p(\mathbf{u})}{k(\mathbf{u})}\, d\mathbf{u},$$

so relative frequencies track the feasible overlap with Σ; under equiprobable environments ($p \equiv \text{const}$) this reduces to the measure of $\Sigma \cap D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ (Grilli et al., 2017, Saavedra et al., 2016*b*, Song et al., 2018*b*). Equal overlap implies equal likelihood, whereas skew in $p(\mathbf{u})$ toward one domain increases its chance of observation. This formulation allows analytical or numerical estimation of $\mathbb{P}(\mathcal{C})$ and ranking of communities by expected frequency, including the identification of maximally feasible configurations under variable conditions (Bartomeus et al., 2021, Deng et al., 2021, Medeiros et al., 2021*a*).

When priority effects are possible, observed frequency is modulated by a history kernel $h_{\mathcal{C}}(\mathbf{u}) \in [0, 1]$ that allocates probability among admissible endpoints under the same $\mathbf{u}$:

$$\mathbb{P}(\mathcal{C}) \;=\; \int_{\Sigma\cap D(\mathcal{C},\mathcal{S},\mathbf{A})} p(\mathbf{u})\, h_{\mathcal{C}}(\mathbf{u})\, d\mathbf{u},$$

with $\sum_{\mathcal{C}} h_{\mathcal{C}}(\mathbf{u}) = 1$ almost everywhere—except on boundary/tie sets of measure zero—on Σ (see Appendix). Here $p(\mathbf{u})$ denotes a probability density on $\Sigma \subset S^{n-1}$ with respect to the $(n-1)$-dimensional surface (Hausdorff) measure σ. Hypothesis 2 is the neutral-history baseline ($h_{\mathcal{C}}$ approximately uniform across admissible candidates), while the integral above provides an immediate bound $\mathbb{P}(\mathcal{C}) \leq \int_{\Sigma\cap D(\mathcal{C},\mathcal{S},\mathbf{A})} p(\mathbf{u})\, du$ and a practical reading: feasibility supplies the environmental support against which history tilts outcomes, and deviations from the baseline quantify the strength and direction of priority effects.

A toy example makes this concrete (uniform p). Suppose the environmental space Σ splits into: an overlap region of measure 0.2 where $\mathcal{C}_1$ and $\mathcal{C}_2$ are both feasible, plus exclusive regions of 0.1 for each community. Then the feasible overlaps are equal: $\sigma(D(\mathcal{C}_1) \cap \Sigma) = \sigma(D(\mathcal{C}_2) \cap \Sigma) = 0.3$, where $\sigma(\cdot)$ denotes surface measure on Σ; for uniform p we report σ–masses as proportions. Under neutral history ($h = 1/2$ in the overlap) both appear with probability $0.1 + 0.5 \times 0.2 = 0.2$.

If history favors $\mathcal{C}_1$ in the overlap ($h_{\mathcal{C}_1} = 0.9,\ h_{\mathcal{C}_2} = 0.1$), obtaining

$$\mathbb{P}(\mathcal{C}_1) = 0.1 + 0.9 \times 0.2 = 0.28 \quad \text{(winner)}, \qquad \mathbb{P}(\mathcal{C}_2) = 0.1 + 0.1 \times 0.2 = 0.12 \quad \text{(loser)},$$

with $\mathbb{P}(\mathcal{C}_1)$ increased by history but still ≤ 0.3, its feasibility-based upper bound.

When long transients are possible (no equilibrium, (Hastings, 2001)), observed frequency is modulated by a finite-time *transient kernel* $v_{\mathcal{C}}(\mathbf{u}; T) \in [0, 1]$ that allocates visibility among communities that are encountered within a window T under the same $\mathbf{u}$ (see Appendix). Let $V_T(\mathcal{C}, \mathcal{S}, \mathbf{A})$ be the set of environmental directions where trajectories spend non-negligible time near $\mathcal{C}$ within T (endpoint feasibility is a special case). We write

$$\mathbb{P}_T(\mathcal{C}) \;=\; \int_{\Sigma \cap V_T(\mathcal{C},\mathcal{S},\mathbf{A})} p(\mathbf{u})\, v_{\mathcal{C}}(\mathbf{u}; T)\, d\mathbf{u},$$

We normalize over the finite-time support

$$\Sigma_T := \bigcup_{\mathcal{C}} V_T(\mathcal{C}, \mathcal{S}, \mathbf{A}), \qquad v_{\mathcal{C}}(\mathbf{u}; T) = \frac{t_{\mathcal{C}}(\mathbf{u}; T)}{\sum_{\mathcal{C}'} t_{\mathcal{C}'}(\mathbf{u}; T)} \quad \text{for} \ \ \mathbf{u} \in \Sigma_T,$$

and set $v_{\mathcal{C}}(\mathbf{u}; T) = 0$ for $\mathbf{u} \notin \Sigma_T$. On boundary/tie sets where the denominator is zero, any measurable tie-break may be used; these sets do not affect integrals. The *neutral-transient* baseline takes $v_{\mathcal{C}}$ approximately uniform across the communities encountered within T at a given $\mathbf{u}$.

A concrete choice that makes $t_{\mathcal{C}}$ and V_T precise is via occupation time of a fixed neighborhood $\mathcal{N}(\mathcal{C})$ of the equilibrium for $\mathcal{C}$:

$$t_{\mathcal{C}}(\mathbf{u}; T) \;=\; \int_0^T \mathbf{1}_{\{\,\mathbf{N}(t;\mathbf{u}) \in \mathcal{N}(\mathcal{C})\,\}}\, dt, \qquad v_{\mathcal{C}}(\mathbf{u}; T) \;=\; \frac{t_{\mathcal{C}}(\mathbf{u}; T)}{\sum_{\mathcal{C}'} t_{\mathcal{C}'}(\mathbf{u}; T)} \quad (\mathbf{u} \in \Sigma_T). \tag{1}$$

Under gradient-like dynamics with a finite collection of hyperbolic attractors (no cycles/chaos) and basins covering Σ up to measure-zero boundaries, $V_T(\mathcal{C}, \mathcal{S}, \mathbf{A}) \to D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ and $v_{\mathcal{C}}(\mathbf{u}; T)$ converges to the history kernel as $T \to \infty$. The expression above yields the bound

$$\mathbb{P}_T(\mathcal{C}) \;\leq\; \int_{\Sigma \cap V_T(\mathcal{C},\mathcal{S},\mathbf{A})} p(\mathbf{u})\, d\mathbf{u},$$

and a practical reading: feasibility supplies the environmental support, while transients add finite-time visibility beyond endpoint support; deviations from the neutral-transient baseline quantify the strength and direction of transient inflation. As $T \to \infty$ and only endpoints matter, $V_T \to D$ and $v_{\mathcal{C}}$ reduces to the history kernel $h_{\mathcal{C}}$. By construction, $V_T(\mathcal{C})$ (and thus Σ_T) is nondecreasing in T; if trajectories settle to endpoints, $V_T(\mathcal{C}) \to D(\mathcal{C})$ as $T \to \infty$.

Another toy example (uniform p). Let Σ have an endpoint overlap of measure 0.2 where $\mathcal{C}_1, \mathcal{C}_2$

are both feasible, plus exclusive endpoint regions of 0.1 for each. Add a *transient corridor* of measure 0.2 where neither is an endpoint but both are commonly visited within *Neutral-transient:* $v_{\mathcal{C}_1} = v_{\mathcal{C}_2} = 1/2$ in both the overlap and the corridor. Then

$$\mathbb{P}_T(\mathcal{C}_1) = 0.1 + 0.5 \times 0.2 + 0.5 \times 0.2 = 0.30 \quad \text{(same for } \mathcal{C}_2\text{)}.$$

Transients favor $\mathcal{C}_1$ *in the corridor:* take $v_{\mathcal{C}_1} = 0.8,\ v_{\mathcal{C}_2} = 0.2$ there (keep 1/2 in the overlap). Then

$$\mathbb{P}_T(\mathcal{C}_1) = 0.1 + 0.5 \times 0.2 + 0.8 \times 0.2 = 0.36, \qquad \mathbb{P}_T(\mathcal{C}_2) = 0.1 + 0.5 \times 0.2 + 0.2 \times 0.2 = 0.24.$$

Here $\mathbb{P}_T(\mathcal{C}_1)$ can exceed its endpoint-feasibility bound 0.3 because the corridor contributes transient visibility; it still respects the transient bound since $V_T(\mathcal{C}_1)$ has total measure 0.5. Therefore, feasibility supplies the environmental support; transients allocate *finite-time visibility* along paths of reassembly. Over-representation of $\mathcal{C}$ relative to its endpoint bound signals strong transient corridors or slow passage near $\mathcal{C}$.

Hypothesis 3 (transition likelihood decreases with environmental distance). Transitions are more likely when two communities are supported by similar environmental directions (Fig. 1). A site-specific measure of proximity is the *feasible overlap*

$$\text{Overlap}(\mathcal{C}_i, \mathcal{C}_j) \;=\; \int_{\Sigma \cap D(\mathcal{C}_i, \mathcal{S}, \mathbf{A}) \cap D(\mathcal{C}_j, \mathcal{S}, \mathbf{A})} p(u)\, du,$$

the probability mass (under the local environments Σ with density $p(\mathbf{u})$) of directions that make both communities feasible. A complementary, geometry-based separation can use *domain centroids*

$$\hat{\mu}_{\mathcal{C}} \;=\; \frac{\int_{\Sigma \cap D(\mathcal{C})} \mathbf{u} p(\mathbf{u})\, d\mathbf{u}}{\left\| \int_{\Sigma \cap D(\mathcal{C})} p(\mathbf{u})\, d\mathbf{u} \right\|}, \qquad d_c(\mathcal{C}_i, \mathcal{C}_j) \;=\; \arccos\!\Big(\hat{\mu}_{\mathcal{C}_i} \cdot \hat{\mu}_{\mathcal{C}_j}\Big),$$

We use angular (great-circle) distances on S^{n-1} for d_c; figures depict geodesic arcs, and chord lengths are a monotone transform of the angle (see Appendix).

which summarize where each domain sits on the unit sphere (Long et al., 2024). In this formulation, transition probability is expected to increase with $\text{Overlap}(\mathcal{C}_i, \mathcal{C}_j)$ and decrease with $d_c(\mathcal{C}_i, \mathcal{C}_j)$, a prediction borne out across systems where reassembly events cluster between communities with overlapping or closely aligned domains (Deng et al., 2024, Saavedra et al., 2016*a*). These quantities compare *environmental support*, not compositional similarity: structurally distinct assemblages can be close (and likely to replace one another) if their domains overlap or point in similar directions, whereas compositionally similar assemblages may be far apart if supported by different environmental directions.

This perspective frames community change as movement along paths of minimal resistance in environmental space—an intuition aligned with least-action ideas (Ferrer-i Cancho and Solé, 2003)—where the "cost" of a transition is approximated by the environmental reorientation needed to move from one domain to another (small d_c, large overlap). See Fig. 2 for an illustration of this process. The geometry of $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$, set by the invariant interaction structure and constrained by physico-chemical laws, thus organizes which transitions are most likely under realized variation (Alberch, 1989, 1991, Solé et al., 2024).

Theoretical support. I next summarize support for the feasibility principle using the gLV model as a characteristic framework. In the unified notation above, theory shows that a community's feasibility domain $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ is an emergent property of the *internal* interaction structure $\mathbf{A}$ (Grilli et al., 2017, Rohr et al., 2014, Saavedra et al., 2016*b*, Song et al., 2018*b*). In particular, $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ is *non-reducible*: it cannot be decomposed additively by richness or by species identity alone (Deng et al., 2022, Saavedra et al., 2017*b*). Adding a new population j (moving from $\mathcal{S}$ to $\mathcal{S} \cup \{j\}$ and from $\mathbf{A}$ to $\mathbf{A}'$) may enlarge or preserve the feasibility domain of the full system, yet the domain of a focal community $\mathcal{C}$ *as embedded in the new pool*, $D(\mathcal{C}, \mathcal{S} \cup \{j\}, \mathbf{A}')$, can rotate or shrink so that it has little or no overlap with its previous embedding $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$. Similar discontinuities arise under deletions and *replacements* (changes in species identity) (Deng et al., 2022, Saavedra et al., 2017*b*, 2016*b*). Thus, higher diversity—or merely different identities—can open new environmental opportunities for $\mathcal{C}$ or erase previously feasible configurations. Under Hypothesis 2, this geometric reshuffling directly alters the frequency of community $\mathcal{C}$, because its observability depends on the overlap between its embedding-specific feasibility domain and the locally realized directions, i.e.,

$$\mathbb{P}(\mathcal{C}) \propto \int_{\Sigma \cap D(\mathcal{C}, \mathcal{S}, \mathbf{A})} p(\mathbf{u}) \, d\mathbf{u},$$

so additions or replacements can increase or decrease expected occurrence even when richness increases.

Empirical support. Experimental work on assembly under changing environments provides empirical corroboration. Specific subsets of populations have been observed to emerge only at later assembly stages (higher diversity), even when those same subsets were not feasible in earlier stages given their earlier embedding in the interaction structure $(\mathcal{S}, \mathbf{A})$ (Angulo et al., 2021, Deng et al., 2021, Saavedra et al., 2017*a*, 2020). Conversely, populations present early can disappear later despite initial feasibility (Angulo et al., 2021, Deng et al., 2021, Saavedra et al., 2017*a*, 2020). These patterns indicate that feasibility is *embedding-dependent*: the domain $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ changes as the species pool and interaction structure evolve.

Collectively, these results reinforce Hypothesis 1: any community $\mathcal{C} \subseteq \mathcal{S}$ is feasible within a specific range of environmental directions, but that range is determined by the *entire* interaction structure. Consequently, communities with similar richness or overlapping membership can have distinct domains $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$. This supports Hypotheses 2–3: as assembly reshapes $\mathbf{A}$ (and thus the geometry of feasibility), observability $\mathbb{P}(\mathcal{C})$ tracks the size of the local overlap $\Sigma \cap D(\mathcal{C}, \mathcal{S}, \mathbf{A})$, and transition likelihoods track the overlap and alignment among domains relevant to realized environmental variation.

Turning to Hypothesis 2—the idea that the probability of observing a community scales with the portion of its feasibility domain that aligns with locally realized environments—there is growing empirical support across systems. In the unified notation, studies on plant–pollinator networks (Cenci et al., 2018, Rohr et al., 2014, Saavedra et al., 2016*b*), plant–herbivore interactions (Medeiros et al., 2021*a*), multi-trophic food webs (García-Callejas et al., 2023), and microbial communities (Deng et al., 2021, Saavedra et al., 2020) consistently find that communities with larger feasible overlap are observed more often, especially when arrival order is randomized or otherwise unbiased (neutral history). Beyond whole-community patterns, species-level analyses show that the probability of observing population i increases with the extent to which the remaining species ($\mathcal{S} \setminus \{i\}$) enlarge i's feasible region (and decreases when the surrounding interaction structure constrains it) (Deng et al., 2021, 2022, Saavedra et al., 2020).

Collectively, these results support the view that feasibility acts as a necessary filter for assembly: communities that are feasible under a broader set of environmental directions occupy a larger "volume" in environmental space and therefore are more likely to arise and persist. This implies that across sites sharing similar $\mathbf{A}$, relative community frequencies should track their feasible overlap with locally realized environments, and that interventions which enlarge this overlap—by altering interaction structure or conditions—should increase establishment and persistence.

Turning to Hypothesis 3—the claim that the likelihood of a transition ($\mathcal{C}_i \to \mathcal{C}_j$) decreases with the environmental distance between their feasibility domains—there is consistent empirical support. Across predator–prey systems (Saavedra et al., 2016*a*), microbial communities (Deng et al., 2024, Long et al., 2024), tree assemblages (Deng et al., 2024), and herbivore communities (Deng et al., 2024, Song et al., 2018*a*), observed reassembly events concentrate between communities whose domains are close in the sense developed above: large feasible overlap in the locally realized environments Σ and small centroid angle $d_c(\mathcal{C}_i, \mathcal{C}_j)$. When the species pool $\mathcal{S}$ is effectively fixed, transitions are most frequently recorded between communities with minimal d_c (operationalized via domain centroids) and substantial overlap in Σ (Long et al., 2024). When the pool or the internal structure shifts through time, transitions tend to favor configurations with larger domains $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ (Deng et al., 2024, Song et al., 2018*a*), consistent with movement toward states that are more compatible or robust under realized environmental variation. Taken together, these patterns support a pathway view of assembly in which reorganization follows "paths of least resistance" in environmental space—small reorientations of $\mathbf{u}$ that carry the system across nearby feasibility boundaries—linking least-action intuitions with the geometry of domains set by the interaction structure $\mathbf{A}$ (Alberch, 1991, Ferrer-i Cancho and Solé, 2003).

Discussion. The story of planet Earth is one of relentless ecological and environmental transformation. Today, however, the pace of change driven by anthropogenic forces is unprecedented, with rates of climate change and habitat modification estimated to be 10–100 times faster than historical baselines (Scheffers et al., 2016). This acceleration demands *predictive* principles for anticipating how communities assemble and reassemble under shifting conditions (Levins, 1968). In this context, the feasibility principle offers a probabilistic guide for conservation and restoration (Cody et al., 1975, Hill et al., 2004, Moreno-Mateos et al., 2017). By Hypothesis 1, each community is characterized by a feasibility domain—set by its internal structure—that determines the range of environmental directions compatible with persistence. Feasible conditions are thus filtered by internal constraints (e.g., species interactions), making the central task to identify both the interaction structure that defines a focal community and the environmental contexts under which it can be maintained (Tabi et al., 2023). Empirical work supports this view: changes in biotic interaction structure that *expand* feasibility domains are associated with increased environmental variability, such as temperature fluctuations (Song et al., 2017, Song and Saavedra., 2020, Tabi et al., 2020). Notably, communities at higher latitudes—subject to greater climatic variability—tend to exhibit broader feasibility domains. Two implications follow. First, for a fixed environment there can exist multiple candidate communities—each with distinct internal structure—that are compatible with that condition. Second, a given community can remain feasible across multiple environments. These implications connect naturally with work on environmental filtering, trait–environment matching, and metacommunity processes, while providing a quantitative map—$D(\mathcal{C}, \mathcal{S}, \mathbf{A})$—to forecast assembly outcomes.

Building on Hypotheses 2 and 3, a practical guidance for intervention emerges. Sequential introductions outperform simultaneous reintroductions in restoration (Deng et al., 2024) because stepwise assembly steers the system through intermediate states with larger domains and greater overlap with local environments, increasing the probability of success at each step. Importantly, the domain of a multi-species community is not the union of its subsets, especially under sequential assembly; trajectories that pass through increasingly feasible configurations are therefore more robust. When several candidate communities have similarly sized domains, choosing the one that requires the smallest environmental reorientation (small centroid distance) or the least structural shift from the current state should further improve success, consistent with "least-resistance" paths in environmental space (Fig. 2). Although much of the present evidence leverages the generalized Lotka–Volterra model, extending the framework by coupling feasibility domains with broader ecological theory (Marquet et al., 2014)—including metabolic and bioenergetic constraints—can clarify how internal limits (interaction structure, physiological bounds) interact with external drivers (temperature, nutrients) (Angulo et al., 2025, Saavedra et al., 2025). Together, these developments point to a unified, testable program for forecasting assembly pathways, identifying likely transitions, and designing interventions under rapid environmental change.

Data and code availability: No new data or code were generated. All previous data and code can be found on Github (`https://github.com/MITEcology`) and the R package feasibilityR (`https://doi.org/10.5281/zenodo.8289566`).

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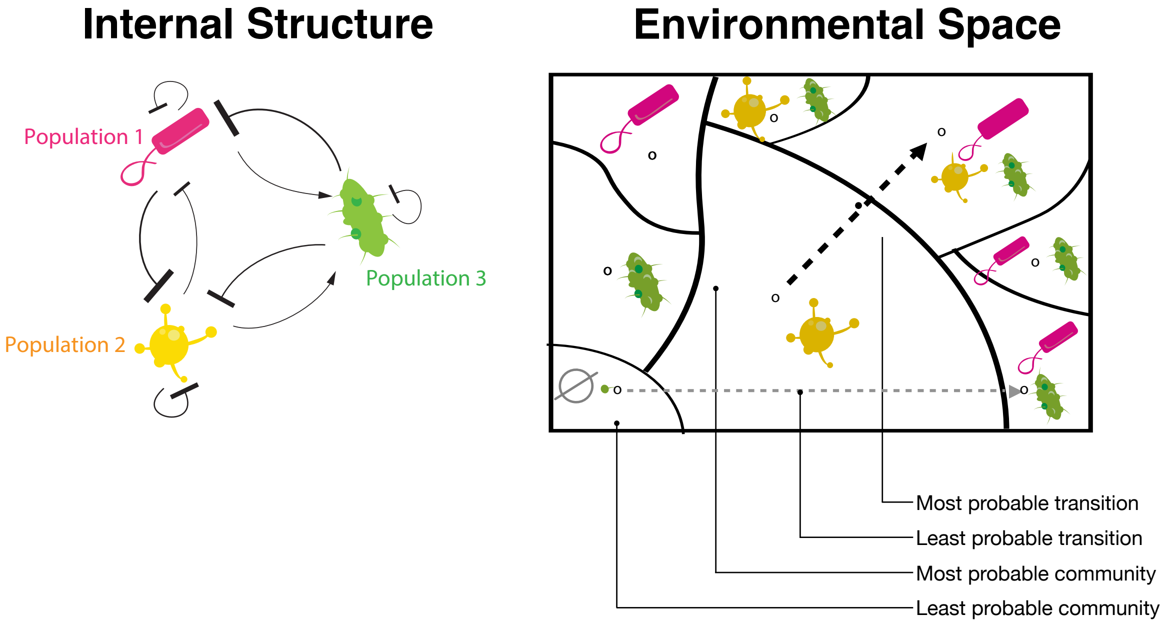

Figure 1: **Graphical representation of the feasibility principle in community ecology**. A central goal of theoretical ecology is to synthesize hypotheses within a quantitative, explanatory, and predictive framework. The feasibility principle offers such a framework by providing a probabilistic understanding of biodiversity patterns across environmental contexts. This principle is composed of three interrelated hypotheses: (i) Ecological communities are feasible within specific regions of environmental space, and these regions are constrained by each community's internal structure (i.e., species interactions define the feasible partition of environmental space). (ii) The probability of observing a particular community is proportional to the size of its feasibility domain that overlaps with locally realized environmental conditions. (iii) Transitions between communities are more likely to occur along paths of least feasible change—i.e., transitions are more probable when communities have larger feasibility domains and smaller distances between those domains in environmental space. In formal models (e.g., the generalized Lotka–Volterra model), the environmental space is defined by environmentally-dependent parameters (e.g., effective growth rates). Each possible community from a given system occupies a distinct region of this space in which it is feasible. These regions are delimited by the system's internal structure. Small circles within each region denote the geometric centers (centroids) of feasibility domains, used to approximate distances between communities.

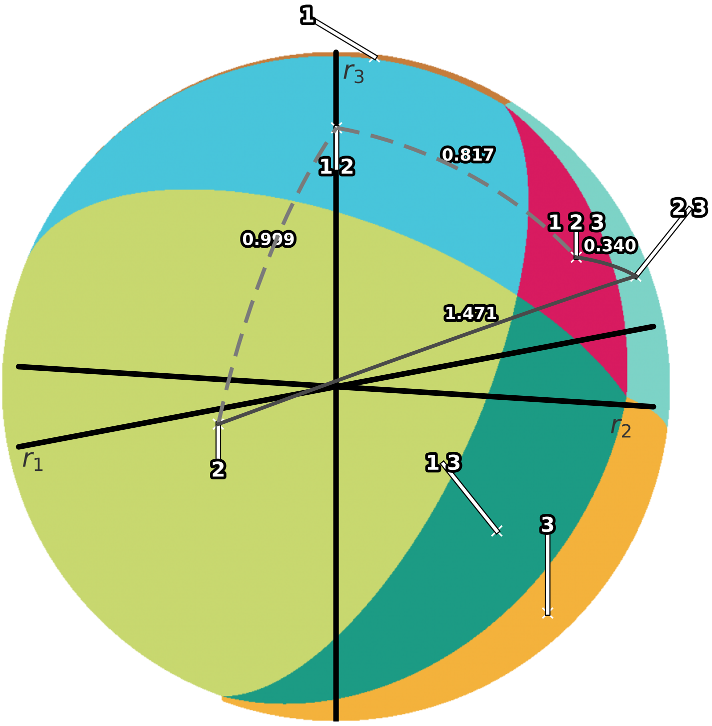

Figure 2: **Graphical representation of least–action path.** Feasibility sphere for the 3-species generalized Lotka–Volterra model. Each point on the unit sphere represents an environment $\mathbf{u}$ (e.g., $u = \mathbf{r}/\|\mathbf{r}\|$) and is colored by the globally attracting composition $\mathcal{C}$ (Deng et al., 2022). White dots mark to feasibility–region centroids. Curves drawn on the sphere are great–circle (geodesic) arcs for visualization, but the numbers shown are *centroid–centroid chord* distances in environmental space (Long et al., 2024). Toy example (arc labels): $d(2, 12) = 0.999$, $d(12, 123) = 0.817$, $d(2, 23) = 1.471$, and $d(23, 123) = 0.341$; the path sums are 1.816 via $\{12\}$ and 1.811 via $\{23\}$, so the shortest-by-distance route is $\{2\} \to \{2, 3\} \to \{1, 2, 3\}$ (dark gray solid; alternative in darker dashed gray).

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Appendix: Mathematical details

Base measure and densities. Let $S^{n-1} \subset \mathbb{R}^n$ be the unit sphere with surface (Hausdorff) measure σ. We fix a measurable subset $\Sigma \subseteq S^{n-1}$ of environmentally admissible directions and take p to be a probability density with respect to σ supported on Σ. Unless stated otherwise, integrals $\int_\Sigma (\cdot)\, d\mathbf{u}$ are shorthand for $\int_\Sigma (\cdot)\, d\sigma(\mathbf{u})$, and "almost everywhere" refers to σ-a.e. on Σ.

gLV implementation and feasibility. In the generalized Lotka–Volterra (gLV) class

$$\dot{N}_i \;=\; N_i\left(r_i(\mathbf{u}) \;+\; \sum_{j\in\mathcal{S}} a_{ij}\, N_j\right), \qquad i \in \mathcal{S}, \tag{2}$$

we take the "environmental" part to enter via $\mathbf{r}(\mathbf{u})$ and the "structural" part via $\mathbf{A} = (a_{ij})$. For $\mathcal{C} \subseteq \mathcal{S}$, denote by $A_{\mathcal{C}\mathcal{C}}$ the principal submatrix on $\mathcal{C}$ and by $r_\mathcal{C}$ the restriction of $\mathbf{r}$. Assume:

(A1) $A_{\mathcal{C}\mathcal{C}}$ is nonsingular for all $\mathcal{C}$ considered;

(A2) self-regulation: $a_{ii} < 0$ for all i;

(A3) regularity: the map $\mathbf{u} \mapsto r(\mathbf{u})$ is measurable on Σ, and for each $\mathcal{C}$, the set $D(\mathcal{C}, \mathcal{S}, mathbf{A}) := \{\mathbf{u} \in \Sigma : \; -A_{\mathcal{C}\mathcal{C}}^{-1} r_\mathcal{C}(\mathbf{u}) \gg 0\}$ is measurable (measurability follows from measurability of $r(\mathbf{u})$ and continuity of the linear map $\mathbf{u} \mapsto -A_{\mathcal{C}\mathcal{C}}^{-1} r_\mathcal{C}(\mathbf{u})$; additional positivity properties (e.g., under M-matrix conditions) are not required for measurability).

When $\mathbf{u} \in D(\mathcal{C}, \mathcal{S}, \mathbf{A})$, define the feasible equilibrium on $\mathcal{C}$ by $N^*_\mathcal{C}(\mathbf{u}) = -A_{\mathcal{C}\mathcal{C}}^{-1} r_\mathcal{C}(\mathbf{u})$ and set $N^*_j = 0$ for $j \notin \mathcal{C}$. We adopt a strict-positivity (open-set) convention for feasibility; boundary points with some $N^*_i = 0$ are allocated to feasibility of the corresponding proper subset and have σ-measure zero under generic conditions.

Non–invasibility and admissible endpoints. Given $\mathbf{u}$, call $\mathcal{C}$ non–invasible if

$$r_j(\mathbf{u}) + \sum_{i\in\mathcal{C}} a_{ji}\, N^*_i(\mathbf{u}) < 0 \quad \text{for all } j \notin \mathcal{C}, \tag{3}$$

with $N^*_\mathcal{C}$ as above. The set of admissible endpoints at $\mathbf{u}$ is $\mathcal{E}(\mathbf{u}) = \{\mathcal{C} : \; \mathbf{u} \in D(\mathcal{C}, \mathcal{S}, \mathbf{A}) \text{ and } \mathcal{C} \text{ is non–invasible}\}$, and $k(\mathbf{u}) = |\mathcal{E}(\mathbf{u})|$. The neutral-history baseline uses $h_\mathcal{C}(\mathbf{u}) = 1/k(\mathbf{u})$ on $\mathcal{E}(\mathbf{u})$ and 0 otherwise. We set $h_\mathcal{C}(\mathbf{u}) = 0$ when $k(\mathbf{u}) = 0$ (i.e., $\mathcal{E}(\mathbf{u}) = \varnothing$).

Centroids and distances. For any feasible $\mathcal{C}$, its (normalized) feasibility centroid is

$$\hat{\mu}_\mathcal{C} \;=\; \frac{\int_{\Sigma\cap D(\mathcal{C})} \mathbf{u}\, p(\mathbf{u})\, d\sigma(\mathbf{u})}{\left\| \int_{\Sigma\cap D(\mathcal{C})} p(\mathbf{u})\, d\sigma(\mathbf{u}) \right\|}, \qquad d_c(\mathcal{C}_i, \mathcal{C}_j) \;=\; \arccos\!\Big(\hat{\mu}_{\mathcal{C}_i} \cdot \hat{\mu}_{\mathcal{C}_j}\Big). \tag{4}$$

We use the angular (great-circle) metric on S^{n-1}; figures depict geodesic arcs for visualization.

Transient kernel via occupation measures. Fix a neighborhood $\mathcal{N}(\mathcal{C})$ for each $\mathcal{C}$ of the subspace where $N_i > 0$ for $i \in \mathcal{C}$ and $N_j = 0$ otherwise. Given a trajectory $\mathbf{N}(t;\mathbf{u})$, define the occupation time

$$t_{\mathcal{C}}(\mathbf{u};T) \;=\; \int_0^T \mathbb{1}\{\mathbf{N}(t;\mathbf{u}) \in \mathcal{N}(\mathcal{C})\}\, dt, \quad \Sigma_T \;=\; \Big\{\mathbf{u} \in \Sigma : \sum_{\mathcal{C}'} t_{\mathcal{C}'}(\mathbf{u};T) > 0\Big\}, \tag{5}$$

and the transient kernel $v_{\mathcal{C}}(\mathbf{u};T) = t_{\mathcal{C}}(\mathbf{u};T)/\sum_{\mathcal{C}'} t_{\mathcal{C}'}(\mathbf{u};T)$ for $\mathbf{u} \in \Sigma_T$, and 0 otherwise. Under gradient-like dynamics with finitely many hyperbolic attractors (no cycles/chaos/heteroclinic wandering), $v_{\mathcal{C}}(\mathbf{u};T)$ concentrates as $T \to \infty$ on the endpoint reached by the dynamics, recovering the endpoint-based expression.