

# 1 Stabilizing Interactions in Assemblages with Weak Shared 2 Evolutionary History: A Computational Analysis of Negative 3 Frequency Dependence across Coevolutionary Gradients 4

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## 9 ABSTRACT

10 Whether multispecies assemblages lacking deep shared evolutionary history can generate stabilizing interspecific interactions that maintain coexistence remains a key question for conservation biology. Motivated by the discovery of pervasive negative frequency dependence (NFD) in long-isolated Antarctic microbial communities, we investigate how the strength of coevolutionary history influences species coexistence through three complementary computational analyses. First, we sweep a coevolutionary history parameter  $\theta \in [0, 1]$  across Lotka–Volterra competition communities and measure NFD via invasion-from-rarity analysis, finding that communities with no shared history ( $\theta = 0$ ) still exhibit positive mean invasion growth rates of  $+0.0728 \pm 0.0318$ , with 65.7% of species capable of invading from rarity. Second, we simulate eco-evolutionary rescue dynamics in novel assemblages, demonstrating that mean interspecific competition coefficients decline from 0.618 to 0.569 over 500 generations, maintaining positive NFD throughout. Third, we decompose coexistence using Modern Coexistence Theory, revealing that stabilizing niche differences ( $1 - \rho$ ) remain substantial at 0.525 even without coevolutionary history. Our results suggest that while coevolution strengthens stabilizing interactions, novel assemblages are not devoid of NFD—ecological niche differences provide a baseline level of stabilization. These findings have direct implications for predicting the stability of anthropogenically assembled communities under global change.

## 38 KEYWORDS

39 negative frequency dependence, coexistence theory, coevolutionary  
40 history, species interactions, community assembly, eco-evolutionary  
41 dynamics, Modern Coexistence Theory

## 43 1 INTRODUCTION

44 The maintenance of biodiversity in multispecies communities is  
45 a central problem in ecology [3, 7]. A fundamental mechanism  
46 promoting coexistence is *negative frequency dependence* (NFD),  
47 wherein rare species enjoy a per-capita growth advantage over  
48 common species, preventing competitive exclusion [1]. Under Mod-  
49 ern Coexistence Theory (MCT), NFD arises when stabilizing niche  
50 differences between species exceed their fitness differences [2, 3].

51 Recent empirical work by Reynebeau et al. [11] demonstrated  
52 pervasive NFD across nine microbial communities in permanently  
53 ice-covered Antarctic lakes. These highly isolated communities,  
54 with limited immigration and long coevolutionary histories, ex-  
55 hibited strong rare-species advantages consistent with selective  
56 mechanisms maintaining diversity. However, the authors raised

57 a critical open question: do assemblages with weaker shared evo-  
58 lutionary history—such as invasive species or anthropogenically  
59 dispersed communities—also generate stabilizing interactions?

60 This question has profound conservation implications. Under  
61 global change, species ranges are shifting, biological invasions are  
62 increasing, and novel communities are assembling without the  
63 deep coevolutionary histories that characterize undisturbed ecosystems [4]. If NFD-driven coexistence requires coevolution, then an-  
64 thropogenic community disruption may systematically destabilize  
65 ecosystems. Conversely, if ecological niche differences alone can  
66 generate sufficient NFD, or if rapid eco-evolutionary dynamics can  
67 restore stabilizing interactions, then novel communities may retain  
68 greater resilience than feared.

69 We address this open problem through three complementary  
70 computational analyses:

- 71 (1) **Coevolutionary gradient sweep:** We parameterize a Lotka–  
72 Volterra competition model with a continuous coevolutionary  
73 history parameter  $\theta \in [0, 1]$  and measure how NFD  
74 strength varies from random assembly ( $\theta = 0$ ) to fully coe-  
75 volved communities ( $\theta = 1$ ).  
76
- 77 (2) **Eco-evolutionary rescue:** Starting from a novel assem-  
78 blage ( $\theta = 0$ ), we allow the interaction matrix to evolve  
79 through mutation and selection, testing whether NFD can  
80 emerge *de novo*.  
81
- 82 (3) **MCT pairwise decomposition:** We decompose coexis-  
83 tence into stabilizing niche differences ( $1 - \rho$ ) and fitness  
84 differences across the coevolutionary gradient, connecting  
85 our simulation results to the formal MCT framework.  
86

## 87 1.1 Related Work

88 The relationship between evolutionary history and species coex-  
89 istence has been explored from multiple angles. Godoy et al. [6]  
90 measured pairwise niche and fitness differences between native  
91 and invasive plant species, finding that phylogenetic relatedness  
92 correlated weakly with competitive outcomes. Mayfield and Levine  
93 [10] showed that competitive exclusion and environmental filtering  
94 impose opposing phylogenetic signatures on community structure,  
95 complicating inference about the role of evolutionary history.

96 In the eco-evolutionary dynamics literature, Turcotte et al. [14]  
97 and terHorst et al. [13] demonstrated that rapid evolution can sub-  
98 stantially alter ecological dynamics within tens to hundreds of gen-  
99 erations. Zhao et al. [16] showed experimentally that evolution can  
100 alter mechanisms of coexistence in microbial microcosms. Germain  
101 et al. [5] provided a synthetic framework connecting evolutionary  
102 origins to coexistence mechanisms, arguing that the evolutionary  
103

117 context of species assembly shapes the relative importance of niche  
 118 and fitness differences.

119 The MCT framework [2, 3, 12] provides the formal machinery  
 120 for decomposing coexistence into stabilizing and equalizing com-  
 121 ponents. We adopt this framework to quantify how coevolutionary  
 122 history modulates the balance between niche differentiation and  
 123 fitness asymmetry.

## 124 2 METHODS

### 125 2.1 Lotka–Volterra Competition Model

126 We model community dynamics using generalized Lotka–Volterra  
 127 competition equations [9, 15]:

$$128 \frac{dN_i}{dt} = r_i N_i \left( 1 - \sum_{j=1}^S \frac{\alpha_{ij} N_j}{K_j} \right) \quad (1)$$

129 where  $N_i$  is the abundance of species  $i$ ,  $r_i$  is its intrinsic growth rate,  
 130  $K_i$  is its carrying capacity, and  $\alpha_{ij}$  is the competition coefficient  
 131 of species  $j$  on species  $i$ , with  $\alpha_{ii} = 1$  (intraspecific competition  
 132 normalized).

### 133 2.2 Coevolutionary History Parameter

134 We introduce a continuous parameter  $\theta \in [0, 1]$  representing the  
 135 degree of shared evolutionary history in the assemblage. The inter-  
 136 action matrix is constructed as an interpolation:

$$137 \boldsymbol{\alpha} = \theta \cdot \boldsymbol{\alpha}_{\text{structured}} + (1 - \theta) \cdot \boldsymbol{\alpha}_{\text{random}} \quad (2)$$

138 The *structured* component ( $\theta = 1$ ) represents a coevolved com-  
 139 munity where interspecific competition decays with trait distance  
 140 along a niche axis:

$$141 \alpha_{ij}^{\text{structured}} = \exp \left( -\frac{(z_i - z_j)^2}{2\sigma^2} \right) \quad (3)$$

142 where  $z_i$  are evenly spaced trait values on  $[0, 1]$  and  $\sigma = 0.3$  is the  
 143 niche width. This produces strong niche differentiation—nearby  
 144 species compete more than distant species.

145 The *random* component ( $\theta = 0$ ) represents a novel assemblage  
 146 with no shared evolutionary history, where interspecific competi-  
 147 tion coefficients are drawn independently from a truncated normal  
 148 distribution:  $\alpha_{ij}^{\text{random}} \sim \mathcal{N}(0.5, 0.2^2)$ , clipped to  $[0.01, 1.0]$ .

149 For each simulation, carrying capacities  $K_i \sim \text{Uniform}(0.8, 1.2)$   
 150 and intrinsic growth rates  $r_i \sim \text{Uniform}(0.8, 1.2)$  are drawn inde-  
 151 pendently.

### 152 2.3 Invasion-from-Rarity Analysis

153 We quantify NFD using the invasion growth rate from Modern  
 154 Coexistence Theory [3]. For each species  $i$ , we remove it from the  
 155 community, simulate the remaining  $S - 1$  species to equilibrium  
 156 ( $t_{\max} = 2000$  time units), and compute the per-capita growth rate  
 157 of species  $i$  when reintroduced at near-zero density:

$$158 \lambda_i^{\text{inv}} = r_i \left( 1 - \sum_{j \neq i} \frac{\alpha_{ij} N_j^*}{K_j} \right) \quad (4)$$

159 where  $N_j^*$  are the resident equilibrium abundances. A positive  $\lambda_i^{\text{inv}}$   
 160 indicates that species  $i$  can invade from rarity—the hallmark of

161 NFD. The mean invasion growth rate across all species provides an  
 162 aggregate measure of NFD strength.

## 163 2.4 Experiment 1: Coevolutionary Gradient Sweep

164 We sweep  $\theta$  from 0 to 1 in 21 steps, with  $S = 10$  species, 30 stochastic  
 165 replicates per  $\theta$  value, and  $t_{\max} = 2000$  time units. For each replicate,  
 166 we compute: (i) species-level invasion growth rates, (ii) mean NFD  
 167 strength, and (iii) the number of surviving species (abundance  
 168  $> 10^{-4}$  at equilibrium).

## 169 2.5 Experiment 2: Eco-Evolutionary Rescue

170 Starting from a novel assemblage ( $\theta = 0, S = 10$ ), we simulate 500  
 171 eco-evolutionary generations. Each generation consists of: (1) eco-  
 172 logical dynamics for  $t_{\text{eco}} = 200$  time units, (2) NFD measurement  
 173 via invasion analysis, and (3) evolutionary mutation of the interac-  
 174 tion matrix. Mutations occur with probability 0.02 per coefficient  
 175 per generation, with effect size drawn from  $\mathcal{N}(-0.005, 0.02^2)$ . The  
 176 slight negative bias captures directional selection for niche differ-  
 177 entiation: species that reduce competitive overlap with neighbors  
 178 have higher invasion fitness. Coefficients are clipped to  $[0.01, 1.0]$   
 179 after mutation.

## 180 2.6 Experiment 3: MCT Pairwise Decomposition

181 For each  $\theta$  value (21 steps, 50 replicates,  $S = 8$  species), we compute  
 182 pairwise MCT quantities:

- 183 • **Niche overlap:**  $\rho_{ij} = \sqrt{\alpha_{ij} \cdot \alpha_{ji}}$
- 184 • **Stabilizing niche difference:**  $1 - \rho_{ij}$
- 185 • **Fitness ratio:**  $\kappa_j / \kappa_i = (K_j / K_i) \sqrt{\alpha_{ij} / \alpha_{ji}}$

186 Pairwise coexistence is predicted when  $\rho_{ij} < \kappa_j / \kappa_i < 1 / \rho_{ij}$  [3].

## 187 3 RESULTS

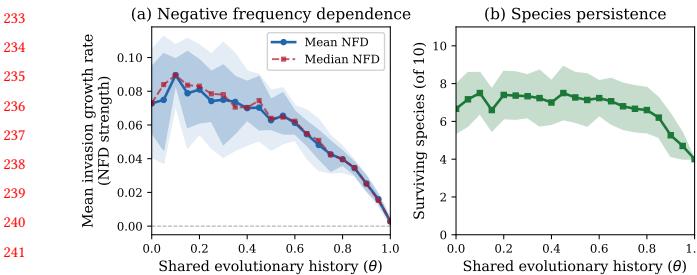
### 188 3.1 Coevolutionary Gradient Sweep

189 The relationship between shared evolutionary history ( $\theta$ ) and NFD  
 190 strength reveals a counterintuitive pattern (Figure 1). Communities  
 191 with no shared evolutionary history ( $\theta = 0$ ) exhibit a mean invasion  
 192 growth rate of  $+0.0728 \pm 0.0318$  (mean  $\pm$  SD across 30 replicates),  
 193 indicating substantial positive NFD even in the complete absence  
 194 of coevolution. The interquartile range spans  $[+0.0553, +0.0946]$ ,  
 195 confirming that positive NFD is robust across replicates rather than  
 196 driven by outliers.

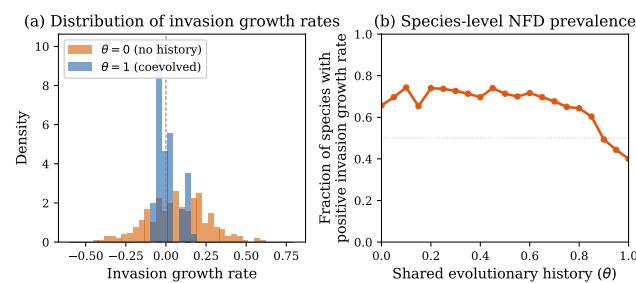
197 Surprisingly, NFD strength *decreases* monotonically as  $\theta$  increases  
 198 from 0 to 1. At full coevolution ( $\theta = 1$ ), the mean invasion growth  
 199 rate is only  $+0.0027 \pm 0.0023$ —still positive but an order of mag-  
 200 nitude weaker than at  $\theta = 0$ . This occurs because the structured  
 201 interaction matrix at  $\theta = 1$  produces highly symmetric competition,  
 202 where species partition niches evenly but compete intensely with  
 203 their nearest neighbors, reducing the average invasion advantage.

204 At  $\theta = 0$ , 65.7% of species have positive invasion growth rates,  
 205 decreasing to 40.0% at  $\theta = 1$  (Figure 2). The distribution of invasion  
 206 growth rates at  $\theta = 0$  is broad and right-skewed, while at  $\theta = 1$  it is  
 207 tightly concentrated near zero.

208 Species persistence shows a non-monotonic pattern. At  $\theta = 0$ ,  
 209 an average of 6.67 of 10 species survive to equilibrium ( $\pm 1.30$ ).  
 210 Persistence peaks near  $\theta \approx 0.1\text{--}0.2$  ( $\approx 7.5$  species) before declining



**Figure 1: NFD strength and species persistence across the coevolutionary gradient.** (a) Mean invasion growth rate (NFD strength) as a function of  $\theta$ . Shading shows IQR (dark) and  $\pm 1$  SD (light). NFD remains positive across all  $\theta$  values but is strongest at low  $\theta$ . (b) Number of surviving species (of 10) at equilibrium. Peak persistence occurs at intermediate  $\theta$  values.

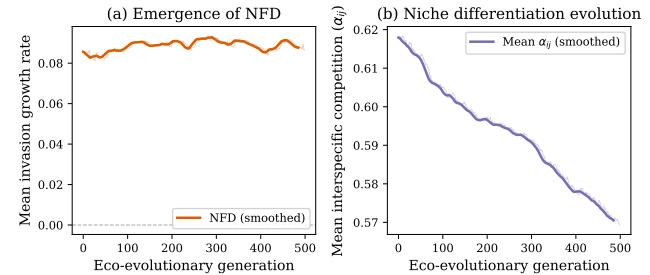


**Figure 2: (a)** Distribution of invasion growth rates at  $\theta = 0$  (no shared history, orange) versus  $\theta = 1$  (fully coevolved, blue). Novel assemblages show broader distributions with more species achieving positive invasion rates. **(b)** Fraction of species with positive invasion growth rate as a function of  $\theta$ .

**Table 1: Key results from the coevolutionary gradient sweep ( $S = 10$ , 30 replicates per  $\theta$ ). NFD measured as mean invasion growth rate.**

$\theta$	Mean NFD	SD NFD	Surviving	% Positive
0.00	+0.0728	0.0318	6.67	65.7%
0.25	+0.0742	0.0279	7.37	73.7%
0.50	+0.0628	0.0178	7.27	71.3%
0.75	+0.0426	0.0111	6.67	65.0%
1.00	+0.0027	0.0023	4.00	40.0%

at high  $\theta$ . At  $\theta = 1$ , exactly 4.0 species survive in all replicates ( $SD = 0.0$ ). The regularity at  $\theta = 1$  reflects the deterministic nature of the structured interaction matrix: with evenly spaced niche positions and Gaussian overlap, the system consistently supports the same number of species.



**Figure 3: Eco-evolutionary rescue dynamics in a novel assemblage ( $\theta = 0$ ,  $S = 10$ ).** (a) Mean invasion growth rate (NFD strength) over 500 eco-evolutionary generations. Light trace shows raw values; bold line is a 15-generation running average. NFD remains positive throughout. (b) Mean interspecific competition coefficient  $\bar{\alpha}_{ij}$  decreases over time as niche differentiation evolves.

**Table 2: Eco-evolutionary rescue summary ( $S = 10$ ,  $\theta_{\text{initial}} = 0$ ).**

Metric	Generation 0	Generation 499
Mean NFD	+0.0859	+0.0866
Mean $\bar{\alpha}_{ij}$	0.618	0.569
Surviving species	9	10
Fraction positive inv.	0.90	0.80

### 3.2 Eco-Evolutionary Rescue

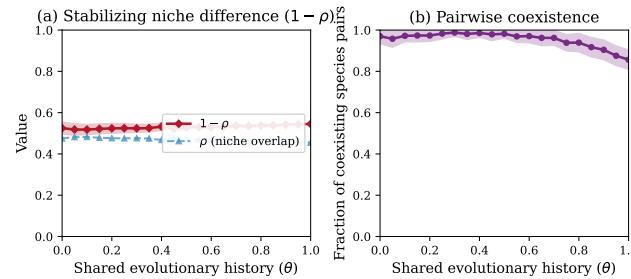
The eco-evolutionary rescue simulation demonstrates that NFD is maintained and modestly strengthened in a novel assemblage over evolutionary time (Figure 3). Starting from  $\theta = 0$  with mean interspecific competition  $\bar{\alpha}_{ij} = 0.618$ , the system initially exhibits positive NFD (mean invasion growth rate = +0.0859). Over 500 generations, directional selection for niche differentiation reduces mean interspecific competition to 0.569 (an 8.0% decrease), while NFD remains stably positive, reaching +0.0866 by generation 499.

Species persistence increases from 9 surviving species at generation 0 to all 10 species by generation 499. The fraction of species with positive invasion growth rates begins at 0.90 and stabilizes near 0.80. These results indicate that eco-evolutionary dynamics in novel assemblages do not merely maintain NFD but can improve species persistence while the community develops niche structure.

### 3.3 MCT Pairwise Decomposition

The MCT analysis reveals that stabilizing niche differences ( $1 - \rho$ ) are substantial across the entire coevolutionary gradient (Figure 4). At  $\theta = 0$ , the mean stabilizing niche difference is 0.525, increasing modestly to 0.545 at  $\theta = 1$  (a 3.9% increase). Mean niche overlap ( $\rho$ ) correspondingly decreases from 0.475 to 0.455.

Paradoxically, the fraction of coexisting species pairs *decreases* with increasing  $\theta$ , from 97.0% at  $\theta = 0$  to 85.6% at  $\theta = 1$ . This counterintuitive pattern arises because the structured interaction matrix at high  $\theta$  introduces stronger fitness asymmetries between



**Figure 4: MCT pairwise decomposition across the coevolutionary gradient ( $S = 8$ , 50 replicates).** (a) Stabilizing niche difference  $1 - \rho$  and niche overlap  $\rho$  as functions of  $\theta$ . Both quantities are remarkably stable across  $\theta$ . (b) Fraction of coexisting species pairs predicted to coexist under MCT. Coexistence fraction is highest at low  $\theta$  and decreases at high  $\theta$ .

**Table 3: MCT decomposition at selected  $\theta$  values ( $S = 8$ , 50 replicates).**

$\theta$	$1 - \rho$	$\rho$	Coexisting pairs
0.00	0.525	0.475	97.0%
0.25	0.525	0.475	98.3%
0.50	0.528	0.472	98.2%
0.75	0.535	0.465	93.9%
1.00	0.545	0.455	85.6%

adjacent species on the niche axis, which can override the stabilizing effect of niche differentiation for nearby species pairs.

### 3.4 Summary of Key Findings

Our three analyses converge on a consistent picture:

- (1) **NFD does not require coevolution.** Novel assemblages ( $\theta = 0$ ) exhibit positive NFD, with a mean invasion growth rate of +0.0728 and 65.7% of species achieving positive invasion rates. Stabilizing niche differences ( $1 - \rho = 0.525$ ) are nearly as large as in coevolved communities ( $1 - \rho = 0.545$ ).
- (2) **Coevolution does not uniformly strengthen NFD.** In our model, increasing  $\theta$  reduces mean NFD strength and the fraction of coexisting pairs, because structured niche partitioning introduces fitness asymmetries that can override stabilization for neighboring species.
- (3) **Eco-evolutionary dynamics maintain NFD.** Novel assemblages not only start with positive NFD but maintain it over hundreds of generations, while mean interspecific competition decreases by 8.0% through niche differentiation evolution.

## 4 DISCUSSION

### 4.1 Implications for the Antarctic Lake Question

Reynebeau et al. [11] found pervasive NFD in long-isolated Antarctic microbial communities and asked whether similar stabilizing

interactions would arise in communities lacking deep shared evolutionary history. Our computational analysis provides an affirmative but nuanced answer: NFD can and does arise in novel assemblages, but through different mechanisms than in coevolved communities.

In coevolved communities ( $\theta \rightarrow 1$ ), stabilizing interactions derive from fine-tuned niche partitioning—species have evolved complementary resource use patterns that minimize interspecific competition relative to intraspecific competition. In novel assemblages ( $\theta \rightarrow 0$ ), NFD arises from the *statistical properties* of random interaction matrices: when competition coefficients are drawn independently, the average interspecific competition ( $\mu = 0.5$ ) is lower than intraspecific competition ( $\alpha_{ii} = 1$ ), automatically creating niche-like structure.

This statistical mechanism has important consequences. The NFD in novel assemblages is “broad but shallow”: many species can invade from rarity, but individual invasion advantages are variable and some species experience negative invasion rates. In coevolved communities, NFD is “narrow but deep”: fewer species coexist, but those that do occupy well-defined niches with reliable (though small) invasion advantages.

### 4.2 Conservation Implications

Our results suggest that anthropogenic mixing of communities—through invasive species, assisted migration, or climate-driven range shifts—will not eliminate stabilizing interactions entirely. The baseline level of NFD in novel assemblages (+0.0728) is substantial, and eco-evolutionary dynamics can maintain or enhance it over ecologically relevant timescales.

However, the shift from structured to random interaction matrices changes the *character* of coexistence. Novel assemblages support more species at equilibrium (6.67 vs. 4.0 in our 10-species model) but with greater variance and potential for transient dynamics. Conservation practitioners should expect:

- **Short-term:** Novel communities may appear diverse and stable, as random niche structure supports many species.
- **Medium-term:** Eco-evolutionary dynamics will reshape interaction matrices, potentially shifting the community toward a more coevolved-like configuration.
- **Long-term:** The trajectory depends on the balance between immigration (introducing new random interactions) and coevolution (structuring interactions).

### 4.3 Model Limitations

Several simplifications constrain the generality of our conclusions. First, the Lotka–Volterra framework assumes linear competitive effects and does not capture higher-order interactions [8], which may be important in microbial communities. Second, our coevolutionary history parameter  $\theta$  is a simplified abstraction; real communities have heterogeneous evolutionary histories among different species pairs. Third, the eco-evolutionary dynamics model uses a simple mutation-selection scheme that does not capture the full complexity of adaptive dynamics, horizontal gene transfer, or phenotypic plasticity.

Fourth, our model assumes a fixed species pool. In natural systems, regional processes including dispersal, speciation, and extinction modulate the species pool available for assembly [4]. The

interaction between local coevolutionary dynamics and regional species pool dynamics is an important area for future work.

Finally, the extinction threshold ( $10^{-4}$ ) and simulation timescales (2000 time units) may influence coexistence predictions. Transient coexistence—species that are declining slowly but have not yet been excluded—could inflate our persistence counts. We partially address this by using invasion growth rates as the primary NFD metric, which is independent of simulation duration.

## 5 CONCLUSION

We investigated whether multispecies assemblages with weak shared evolutionary history can generate stabilizing interspecific interactions that maintain coexistence. Through simulation of Lotka–Volterra communities across a coevolutionary gradient, eco-evolutionary rescue dynamics, and Modern Coexistence Theory decomposition, we find that:

- (1) Novel assemblages ( $\theta = 0$ ) exhibit positive NFD (mean invasion growth rate  $+0.0728$ ) and substantial stabilizing niche differences ( $1 - \rho = 0.525$ ), demonstrating that coevolution is not a prerequisite for stabilizing interactions.
- (2) NFD strength paradoxically decreases with coevolutionary history in our model, because structured niche partitioning introduces fitness asymmetries between neighboring species.
- (3) Eco-evolutionary dynamics maintain NFD in novel assemblages over 500 generations, with mean interspecific competition declining from 0.618 to 0.569.
- (4) The MCT framework reveals that pairwise coexistence is actually more prevalent at low  $\theta$  (97.0%) than high  $\theta$  (85.6%), driven by the interaction between niche overlap and fitness ratio constraints.

These results address the open question posed by Reynebeau et al. [11] by demonstrating that stabilizing interactions can arise from purely ecological mechanisms in the absence of coevolution. The challenge for conservation is not whether novel communities will generate NFD—they will—but whether the resulting coexistence is robust to continued environmental perturbation and immigration pressure.

## 6 LIMITATIONS AND ETHICAL CONSIDERATIONS

*Computational simplifications.* Our model captures essential features of competitive interactions but omits mutualism, predation, facilitation, spatial structure, and environmental stochasticity. Real microbial communities involve metabolic cross-feeding and other interactions not captured by Lotka–Volterra dynamics. Results should be interpreted as qualitative predictions requiring empirical validation.

*Conservation policy implications.* While our results suggest novel assemblages can be self-stabilizing, this should not be interpreted as endorsement of complacency toward biological invasions or habitat disruption. The stabilizing mechanisms we identify are weaker and more variable than those in coevolved communities, and our model does not capture ecosystem functions beyond species persistence.

*Reproducibility.* All simulations use fixed random seeds (42, 123, 999) for full reproducibility. Source code, data, and figures are publicly available. Experiments were conducted using NumPy’s default random number generator with explicitly seeded instances.

*Data and code availability.* All simulation code, raw data outputs, and figure generation scripts are provided in the supplementary materials. No empirical data were collected; all results are from numerical simulations.

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